

Biogeography of the Order Carnivora

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By definition, a carnivore is a flesh-eater (L., *carnis*, flesh; *vorare*, to devour). In the widest sense, the term refers to organisms that prey upon animals, and thus may include vertebrate and invertebrate predators and even insectivorous plants. Insects constitute an enormous source of animal protein, and the many species of primarily insectivorous mammals that have exploited this resource during the Cenozoic could be termed carnivores. In this chapter, however, I restrict the term "carnivore" to the three great global radiations of Cenozoic therian mammals that have exploited predation on, and/or scavenging of, vertebrates as a principal feeding mode: (1) predaceous marsupials; (2) among the placentals, the creodonts, and (3) the true Carnivora (here termed *carnivorans*, following Van Valen [1969], to distinguish them from carnivorous mammals in general). These three groups have been formally classified at various times as mammalian orders of coordinate rank: (1) Marsupicarnivora; (2) Creodonta; (3) Carnivora. I designate the three simply as marsupial carnivores, creodonts, and carnivorans. My primary focus will be the biogeography of placental carnivorans (Order Carnivora); more detailed treatment can be found, for marsupial carnivores, in Archer (1976) and Marshall (1976, 1978a), and, for creodonts, in Barry (1988), Denison (1938), Gingerich and Deutsch (1989), Ginsburg (1980), Gunnell and Gingerich (1991), Lange-Badré (1979), Lange-Badré and Haubold (1990), Mellett (1977), and Springhorn (1980).

During the Cenozoic, the evolution of terrestrial carnivores is manifested in a number of adaptive radiations geographically confined to northern and southern continental areas: (1) North America–Eurasia; (2) South America–Antarctica–Australia; (3) Africa. An excellent Cenozoic record of fossil carnivores, coupled with the geographic isolation of these radiations, allows us to observe multiple natural experiments in the evolution of terrestrial mammalian predators. Marsupial carnivores dominate the Cenozoic faunas of Australia and South America, and may have flourished in Antarctica. A radiation of

marsupial carnivores (Borhyaenidae, 33 genera including Thylacosmilinae) and large phororhacoid birds developed in South America from the Paleocene until the Pliocene, when placental carnivorans entered from the north (Marshall 1978a, b, 1985). In Australia, marsupial carnivores of the families Dasyuridae and Thylacinidae attained a diversity of about 19 genera (Marshall 1981), none of large body size, the niche for large carnivores having been filled in part by giant varanid lizards, crocodilians, and boid snakes.

Placental carnivores radiated first in the early Cenozoic as creodonts, and then in the early to late Cenozoic as carnivorans, both groups confined to the northern continents (Eurasia, North America) and Africa. Africa's early Cenozoic fossil record is poorly known; the oldest African carnivores are represented only by rare, indeterminate teeth from the Paleocene. The first well-sampled African carnivore fauna, of Oligocene age, includes only creodonts; the earliest carnivoran diversity appears in the early Miocene rift sediments of East Africa, and these carnivorans are still accompanied by creodonts, in some numbers. But from at least the beginning of the Pliocene to the present, the carnivorans have been the dominant African predators. However, the endemic carnivore fauna of Africa remains in doubt because of the limited number of early Cenozoic sites and some uncertainty in distinguishing Eurasian immigrants from native lineages.

Late in the Cenozoic, the marsupial sanctuary in the austral salient is finally violated by the immigration of placental carnivorans into South America, by human introduction of placental carnivorans into Australia, and by probable local extinctions in Antarctica caused by the development of the continental ice cap.

Biogeography of the Order

Recent progress in our understanding of carnivoran phylogeny has made possible a marked clarification in the biogeography of the order. Studies utilizing the basicranium, teeth, and feet of extinct and living Carnivora have supplied reliable taxonomic units with clear distributional patterns. Since 1965 the sampling of middle to late Cenozoic fossil Carnivora has been enriched by access to the American Museum's Childs Frick collection (New York), accumulated in North America primarily during the late 1920s to 1965; by energetic collecting and continual refinement of the European fossil mammal record; and by the inauguration of intensive Cenozoic explorations in western and southern Asia, China, and Africa. In broad outline, the biogeographic history of the major groups of carnivorans is now evident, and merits review. The information thus marshaled should be useful in the study of other mammalian groups, whose distribution and ecological relationships were frequently influenced by the biogeographic evolution of carnivorous mammals.

I discuss carnivoran biogeography here in terms of the major divisions of the order first outlined by the English zoologist W. H. Flower (1869). Today, these

three divisions are usually accorded subordinal rank, and include the various living and †extinct families: Arctoidea (Ursidae, †Amphicyonidae, Otariidae, Phocidae, Odobenidae, Mustelidae, Procyonidae); Cynoidea (Canidae), Aeluroides (Felidae, Viverridae, Herpestidae, †Nimravidae). Current informed opinion recognizes the arctoids and cynoids as sister-taxa, together constituting the Caniformia, and the aeluroids constitute the Feliformia.

The biogeography of arctoids, cynoids, and aeluroids can be confidently set forth for the middle and late Cenozoic, that is, for the Oligocene to Recent. Some of these lineages can also be recognized in the later Eocene, but in general the tracking of middle and late Cenozoic lineages into the early Cenozoic (Paleocene and Eocene) has been a frustrating and often unsatisfactory process. A principal reason for this difficulty has been the scarcity of good cranial material of Paleo-Eocene Carnivora (only a single skull with basicranium of a Paleocene carnivoran is known). Despite these problems, however, two major groups of early Cenozoic carnivorans, the Miacidae and Viverravidae, can be identified, primarily on the basis of dental traits. As the only carnivorans currently known from Paleocene rocks, viverravids claim the place of oldest members of the order. Miacids, which first appear in the earliest Eocene, are the most abundant of the Eocene Carnivora despite coexistence with viverravids during most of the epoch. The geographic distribution of miacids and viverravids is not particularly revealing: both groups are found on the northern continents, but the record is so poor on the southern landmasses that little can be concluded about their early distribution or areas of origin. Most miacids and viverravids occur in three geographic regions: fossils from (1) western North America are more abundant and complete than the sparse record of (2) western Europe and (3) China, where both families are represented largely by fragmentary dental remains.

Thus it is the chronicle of the Oligocene to Recent Carnivora that will be set forth in this chapter in an attempt to clarify the distribution and migrations of major carnivoran families during the middle and late Cenozoic. The biogeographic history and distributions of these carnivoran families, presented in Figures 15.3–9 and 15.11–16, emphasize the Neogene record.

Biogeography of the Arctoids

Arctoids, the carnivorans of the northern continents (the Holarctic region), dominate the faunas of Eurasia and North America from the late Eocene to Recent. Their history is one of Holarctic regional evolution *in situ* coupled with migration events southward into Africa and South America. Members of the Arctoidea attain the largest body size in the order (the Pleistocene ursid *Arctodus*) and the smallest (the living mustelid *Mustela nivalis*, the least weasel).

Their early diversity is best recorded in the fossil faunas of the Phosphorites du Quercy, France, where numerous lineages of small to mid-sized arctoids

were preserved in late Eocene to Oligocene fissure fillings (Remy et al. 1987; Teilhard 1915). Early arctoids, for example certain White River Group amphicyonids in the midcontinent (Hunt, in press, c) are in some cases abundant in the late Eocene to Oligocene of North America, but the Nearctic record lacks the diversity of lineages seen in Europe at this time (Bryant 1993; Emry 1992; Gustafson 1986). The early Asian arctoid record is poorer than that in North America, and very few specimens are yet known (Russell and Zhai 1987). The richest sample in Asia derives from the early Oligocene of Hsanda Gol in Mongolia. Hsanda Gol's few arctoids are comparable to lineages from Quercy in Europe, suggesting a Palaearctic commonality.

Four arctoid families can be recognized: Ursidae, Amphicyonidae, Mustelidae, and Procyonidae. Pinnipeds, also derived from an arctoid stock (Hunt and Barnes 1994; Mitchell and Tedford 1973), comprise three families: Otariidae, Odobenidae, and Phocidae.

Ursidae

Ursids living today are widely distributed across Eurasia and North America, and are also present in northwestern South America. The living ursids are a highly uniform group in terms of their general postcranial anatomy, basicranial and auditory structure, and dental features. In the past, however, ursid diversity was much richer in species and more varied in postcranial adaptations, body size, and teeth.

The living bears are all placed in the Ursinae (Tribe Ursini), with the exception of the spectacled bear, *Tremarctos ornatus*, of South America (Ursinae, Tribe Tremarctini) and the giant panda, *Ailuropoda melanoleuca*, of southeast Asia (Ailuropodinae). Although an ursid, the giant panda has had a long, separate history of evolution relative to the ursine bears. It descends as a distinct lineage from the late Miocene protopanda *Ailurarctos* (7–8 Ma, Turolian, Lufeng, China), whose teeth already display the beginnings of the elaborate cusps so spectacularly developed in the living giant panda (Qiu and Qi 1989). The tribes Ursini and Tremarctini are related, probably sharing a common ancestor in the small early and middle Miocene ursid *Ursavus* from Eurasia and North America.

G. G. Simpson's concept of the Ursidae (Simpson 1945) included only the living ursine bears and a few extinct relatives, all characterized by morphological uniformity in the postcranial skeleton, cranium, and teeth, and by their ambulatory plantigrade style of locomotion. Today, ursids are seen in a broader and more inclusive perspective derived from new paleontological evidence: the family comprises a series of three middle to late Cenozoic radiations (Amphicyonodontinae, Hemicyoninae, and Ursinae) that more accurately reveal the Ursidae as an arctoid group experimenting with

both cranial and postcranial functional strategies throughout their 40-million-year history (Hunt, in press, a).

Amphicyodontines and hemicyonines include a varied array of extinct ursids that dominated the arctoid fauna of the northern continents in the Oligocene and Miocene. Simpson (1945), who listed 14 ursid genera in his classification of the family, included primarily the living ursines, and omitted the amphicyodonts and hemicyonines altogether. Moreover, he classified amphicyodonts and hemicyonines as canids, not ursids, owing to the mistaken practice at that time of using teeth as the principal index of relationships.

Simpson failed to recognize that ursids are united by a common basicranial pattern different from that found in true canids (Hunt 1974a, b, 1977). The auditory bulla pattern in living ursids is Type A (Hunt 1974a), believed to be representative of the plesiomorphic arctoid state (Figure 15.1). The Type A bulla is formed primarily by an ectotympanic. A rostral entotympanic element occupies the anterointernal corner of the bulla (enclosing the internal carotid artery), and a small, elongate, elliptical caudal entotympanic (E1) is attached to the medial rim of the ectotympanic. In addition, the posterointernal corner of the bulla is closed by a very small, cup-shaped caudal entotympanic (E2). In the adult the ectotympanic and the three entotympanic elements fuse together into a unit structure in which the sutures joining the elements may or may not be distinguishable. Most important, however, is that the relative contribution of each of these elements to the bulla does not change significantly during ontogeny. This situation is in marked contrast to that in true canids, in which the caudal entotympanic is a single element that strongly inflates during ontogenetic development to form the highly distinctive and recognizable bulla shape common to all living and extinct Canidae (Hunt 1974a, b).

In addition to the Type A auditory bulla, ursids also share a deeply embayed basioccipital bone that in living species contains a loop of the internal carotid artery nested within the inferior petrosal venous sinus (Figure 15.2). This artery-vein complex is believed to be a countercurrent heat-exchange device cooling arterial blood flowing to the brain (Hunt 1977, 1990; Hunt and Barnes 1994). Extinct ursids possess embayed basioccipital bones, presumably containing an expanded venous sinus that could have housed at first a rudimentary, later a more developed, loop of the internal carotid. Living and extinct canids do not show embayed basioccipitals, nor do living species have a carotid loop.

Finally, most ursids (a few amphicyodonts with primitive molars are exceptions) have upper molars in which the crown is quadrate (subquadrate in some amphicyodonts and some species of *Cephalogale*), with four principal cusps (protocone, paracone, metacone, metaconule). The metaconule is enlarged and connected to the protocone by an anteroposterior ridge. The protocone basin opens to the rear and is not closed by a postprotocrista (except in a few dentally plesiomorphic amphicyodonts and species of *Cephalogale* in which the metaconule is not enlarged and a normal postprotocrista closes the proto-

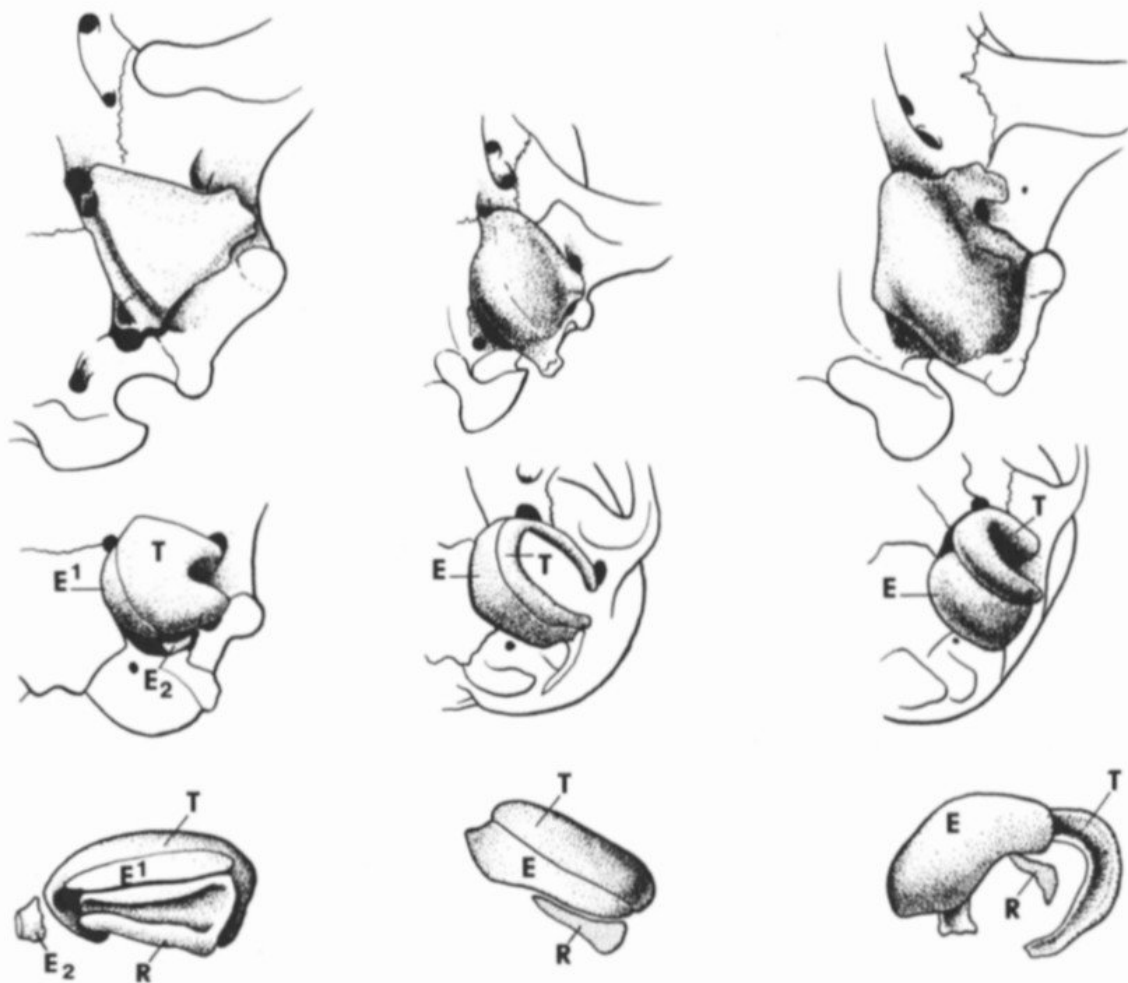


Figure 15.1. Ontogenetic elements forming the auditory bulla in (left to right) arctoid (ursid), cynoid (canid), and aeluroid (felid) carnivorans. *Top row:* adult basicrania with left auditory bulla in ventral view; *middle row:* neonatal stage, same view showing ectotympanic (T) and caudal entotympanic (E) elements that unite to form the adult bulla; *bottom row:* neonatal bullae in medial view (anterior to right), removed from skull to show relationship of rostral entotympanic (R, not visible in ventral view) to ectotympanic and caudal entotympanic elements. Two caudal entotympanics (E1, E2) are present in ursids. (After Hunt and Tedford 1993.)

cone basin). This molar pattern accompanies a retracted protocone on the upper carnassial and often low simple premolars surrounded by distinct cingula. The migration of the metaconule to the posterointernal corner of the tooth (Beaumont 1982) and the open protocone basin are useful diagnostic traits of ursid molars. In ursine ursids, the posterior border of M2 enlarges (rudimentary in some *Ursavus* and *Agriotherium*) and elongates to form a prominent talon not seen in amphicyonodonts and hemicyonines. Ursids never evolve greatly enlarged crushing premolars, nor do they develop the hypersectorial carnassial blades generally seen in felids and hyaenids. Tooth-wear facets on the carnassials and molars of large hemicyonines and living ursines (Ursini) indicate that the former retained some shear in their bite, but the latter use the teeth primarily for crushing, an interpretation supported by the strong reduction in size of the carnassial teeth in Ursini.

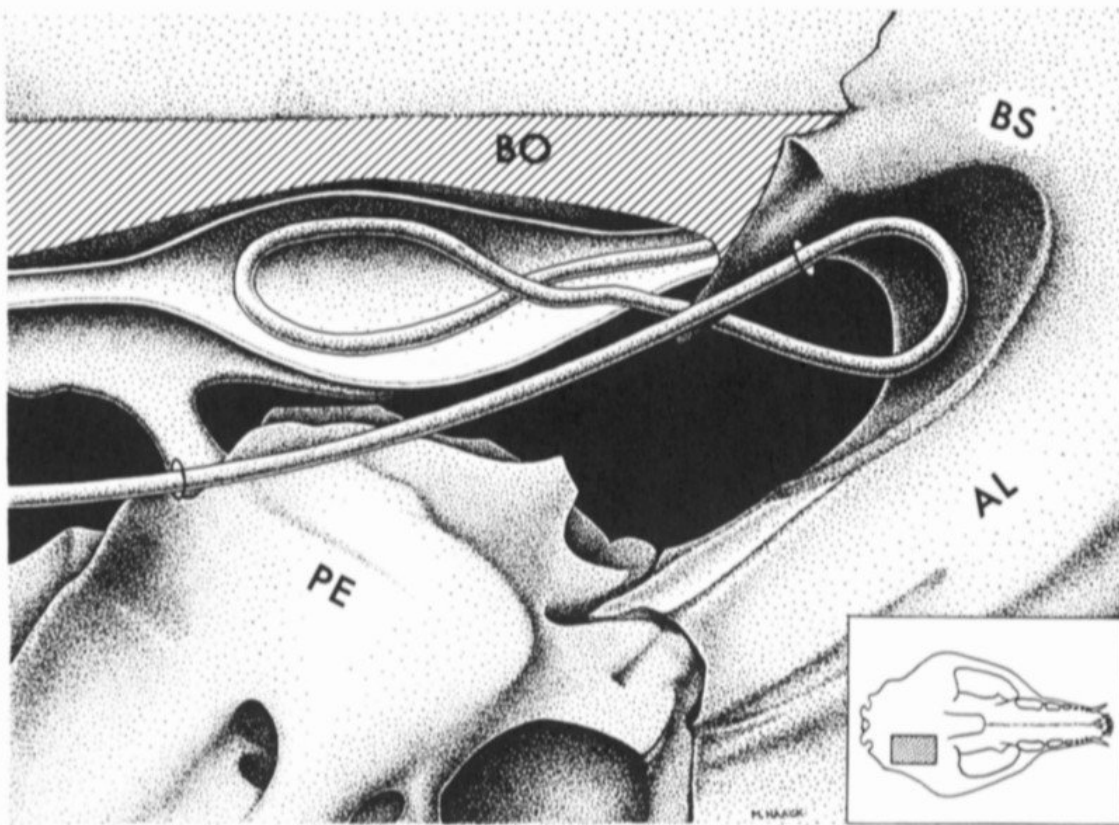


Figure 15.2. Auditory region of a living ursid, demonstrating the looped internal carotid artery nested within the inferior petrosal venous sinus. The sinus is emplaced in the lateral margin of the basioccipital bone. In the illustration the left side of the basioccipital has been removed to show the artery-vein complex, and the venous sinus has been opened to show the arterial loop within. Small circles around the artery show the locations of the anterior and posterior carotid foramina: the segment of the artery between the circles lies within the medial wall of the auditory bulla. Abbreviations: BO, basioccipital; BS, basisphenoid; AL, alisphenoid; PE, petrosal. (After Hunt 1977.)

Amphicyonodonts are a paraphyletic late Eocene-Oligocene stem group from which evolved all other ursids (the last amphicyonodonts are extinct by the end of the early Miocene). They are small in body size (<15 kg except for the large North American aquatic amphicyonodont *Kolponomos*), but the basicranium and plesiomorphic dental pattern of the Ursidae are already evident. The earliest amphicyonodonts are more diverse and better represented in Europe than in Asia or North America (Figure 15.3). The core genera in Europe are *Amphicyonodon* and *Pachycynodon*, both well represented in the Quercy fissures (Teilhard 1915; Cirot and Bonis 1992). North American amphicyonodonts have been placed in *Parictis* and are not yet identified in Eurasia; they occur only in the White River Group of the Great Plains and northern Rocky Mountains, and in the John Day beds of Oregon (Clark and Guensburg 1972). In Asia the only amphicyonodonts belong to *Amphicyonodon* and the small but derived *Amphicticeps*, both from the Oligocene Hsanda Gol Formation of Mongolia; the latter genus seems to be a plausible ancestor for the highly specialized North American amphicyonodonts *Allocyon* and *Kolponomos* of the Pacific Northwest, *Allocyon* known from a single individual (Merriam

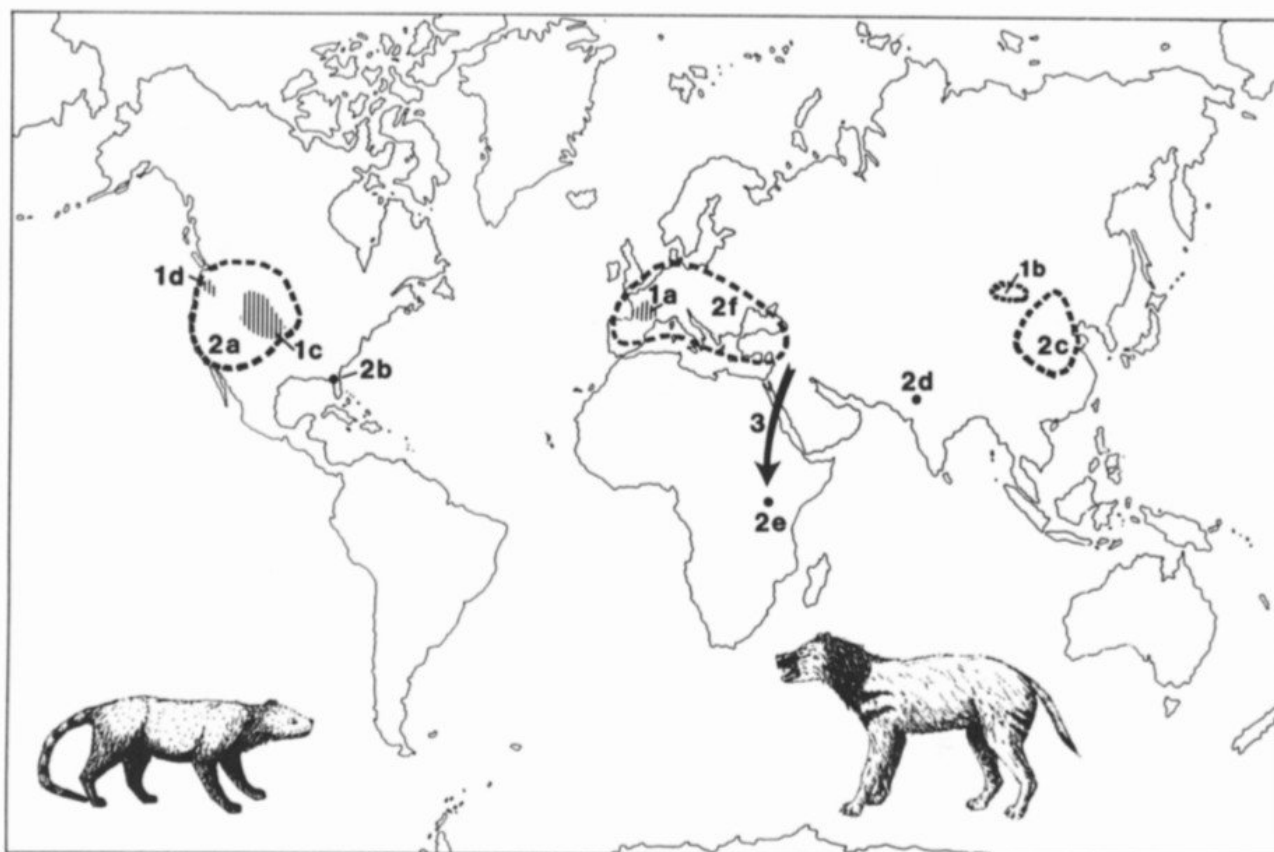


Figure 15.3. Geographic distribution of Late Eocene, Oligocene, and Miocene fossil ursids (Amphicyonodontinae, Hemicyoninae). 1, amphicyonodontines: 1a, western Europe (*Amphicyonodon*, *Pachycynodon*); 1b, Mongolia (*Amphicyonodon*, *Amphicticeps*); 1c, White River Group of the Great Plains and Rocky Mountains, North America (*Parictis*); 1d, John Day beds, Oregon (*Parictis*, *Allocyon*); Washington (*Kolponomos*). 2, hemicyonines: 2a, western United States (*Plithocyon*, *Cephalogale*, undescribed genus); 2b, Florida (*Phoberocyon*); 2c, eastern China (*Hemicyon*, *Phoberocyon*); 2d, Dera Bugti, Pakistan (*Cephalogale*); 2e, Rusinga, Kenya (hemicyonine); 2f, Europe and Asia Minor (*Hemicyon*, *Plithocyon*, *Phoberocyon*, *Dinocyon*, *Cephalogale*). 3, early Miocene migration of hemicyonines into east Africa about 18 Ma.

1930), *Kolponomos* from only three (Stirton 1960; Tedford et al. 1991). Since there are no records of amphicyonodonts on the southern continents, at present they remain a Holarctic group.

Hemicyonines are mid-sized to large carnivorous ursids (5 to >200 kg), but in contrast to ursines and amphicyonodonts they show pronounced cursorial adaptations of the postcranial skeleton. The principal derivative feature of the group is a digitigrade stance in which both the metatarsals and metacarpals are elongate; because the major weight-bearing axis passes between digits 3 and 4, the foot is functionally paraxonic.

Hemicyonines were an Oligocene-Miocene group, becoming extinct by the end of the late Miocene (Figure 15.3). The Miocene hemicyonine radiation (*Hemicyon*, *Plithocyon*, *Phoberocyon*, *Dinocyon*, *Cephalogale*) includes the first ursids to attain large body size. These bears were long thought to be members of the Canidae, but their basicrania and teeth demonstrate unequivocally

cally that they are long-footed ursids with well-developed running ability and carnivorous dentitions. Cursorially adapted Old and New World hemicyonines paralleled the cursorial predatory canids evolving in the New World during the Miocene.

Hemicyonines were found only in Eurasia and North America, until a single tooth was reported from the early Miocene of East Africa (Schmidt-Kittler 1987). These, then, are evidently the first ursids to invade the southern continents, and probably a richer record of the group will emerge in future years from Africa.

The Ursinae are here divided into three tribes: Ursavini, Ursini, and Tremarctini. The Tremarctini and Ursini include all living ursids (except the giant panda), and are the product of relatively recent Plio-Pleistocene ursid radiations. A separate tribe, the Ursavini, is suggested for the Holarctic Miocene ursines (Figure 15.4): the large *Agriotherium* and *Indarctos* and the small, ancestral ursine *Ursavus*.

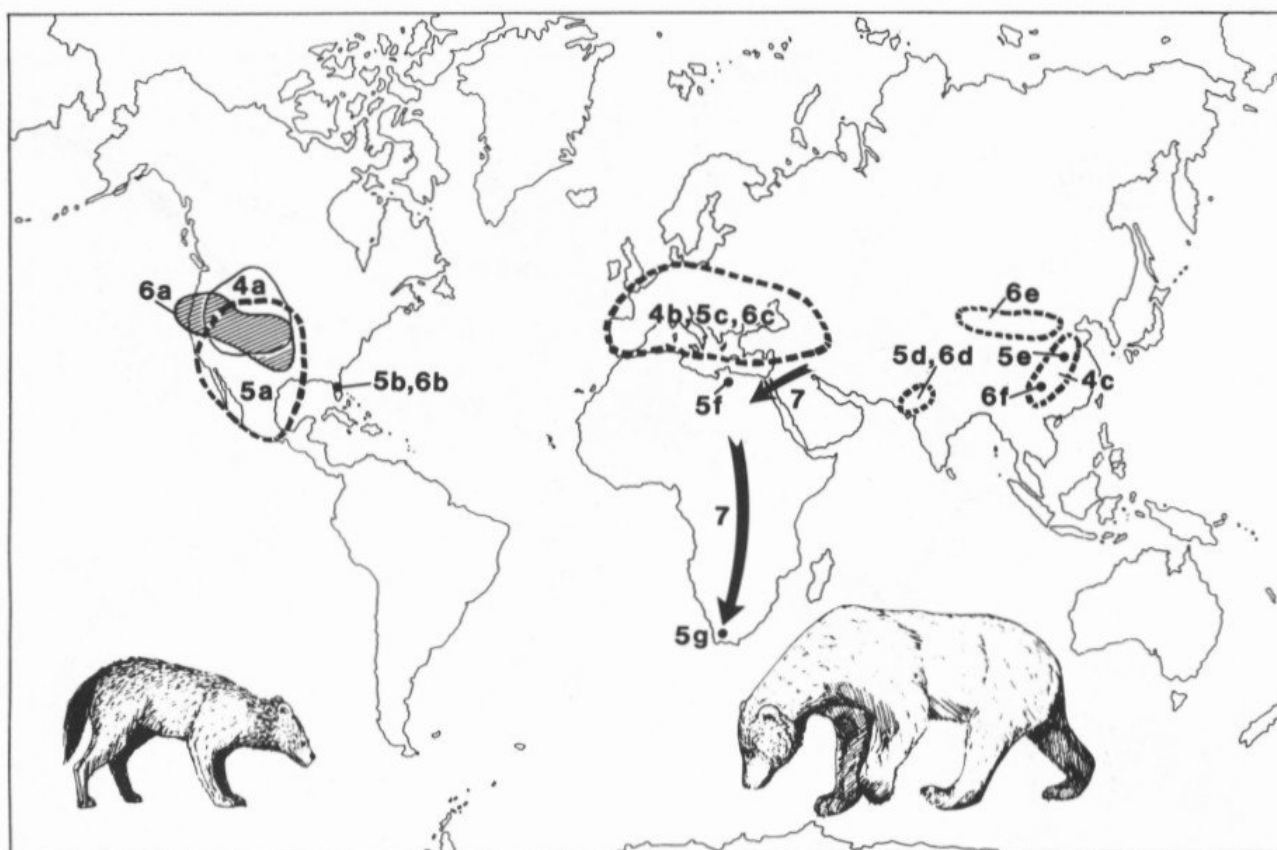


Figure 15.4. Geographic distribution of Miocene fossil ursids (Ursavinae). 4, *Ursavus*: 4a, western United States and Canada; 4b, Europe and western Asia; 4c, eastern China (Shanwang, Lufeng). 5, *Agriotherium*: 5a, western United States and Mexico; 5b, Florida (Bone Valley); 5c, Europe and western Asia (to Iran); 5d, Siwalik Group; 5e, Xiaoxian fissure, China; 5f, Libya (Sahabi); 5g, south Africa (Langebaanweg). 6, *Indarctos*: 6a, western United States; 6b, Florida; 6c, Europe and western Asia; 6d, Siwalik Group; 6e, north China; 6f, south China (Lufeng). 7, latest Miocene to early Pliocene migration of *Agriotherium* into Africa.

The theater of ursid evolution has been the northern continents. Only the ursine bears have effectively migrated into Africa and South America, and these migrants are commonly large, predaceous ursids. But despite their penetration into the southern continents, they achieved only limited species diversity. *Arctodus* is the first ursid to reach South America, appearing in Argentinian deposits judged to be younger than 2 Ma and containing other North American immigrant mammals (Marshall 1985; Kurtén 1967). In Africa, the large agriotheres (*Agriotherium*), which range from Libya (Boaz et al. 1979) to South Africa (Hendey 1980) in the earliest Pliocene, are the only ursids known to have spread over the African continent. *Ursus* enters North Africa in the Pleistocene (Hopwood and Hollyfield 1954), but there is no evidence that the genus spread beyond this limited area: *Ursus arctos* is said to have disappeared from northwest Africa during the mid-nineteenth century (Nowak 1991:1091).

Tremarctini includes the ancestral *Plionarctos*, which is confined to western North America, and its probable descendants *Tremarctos* and *Arctodus* (Figure 15.5). *Plionarctos* first appears ~7 Ma in North America in the late

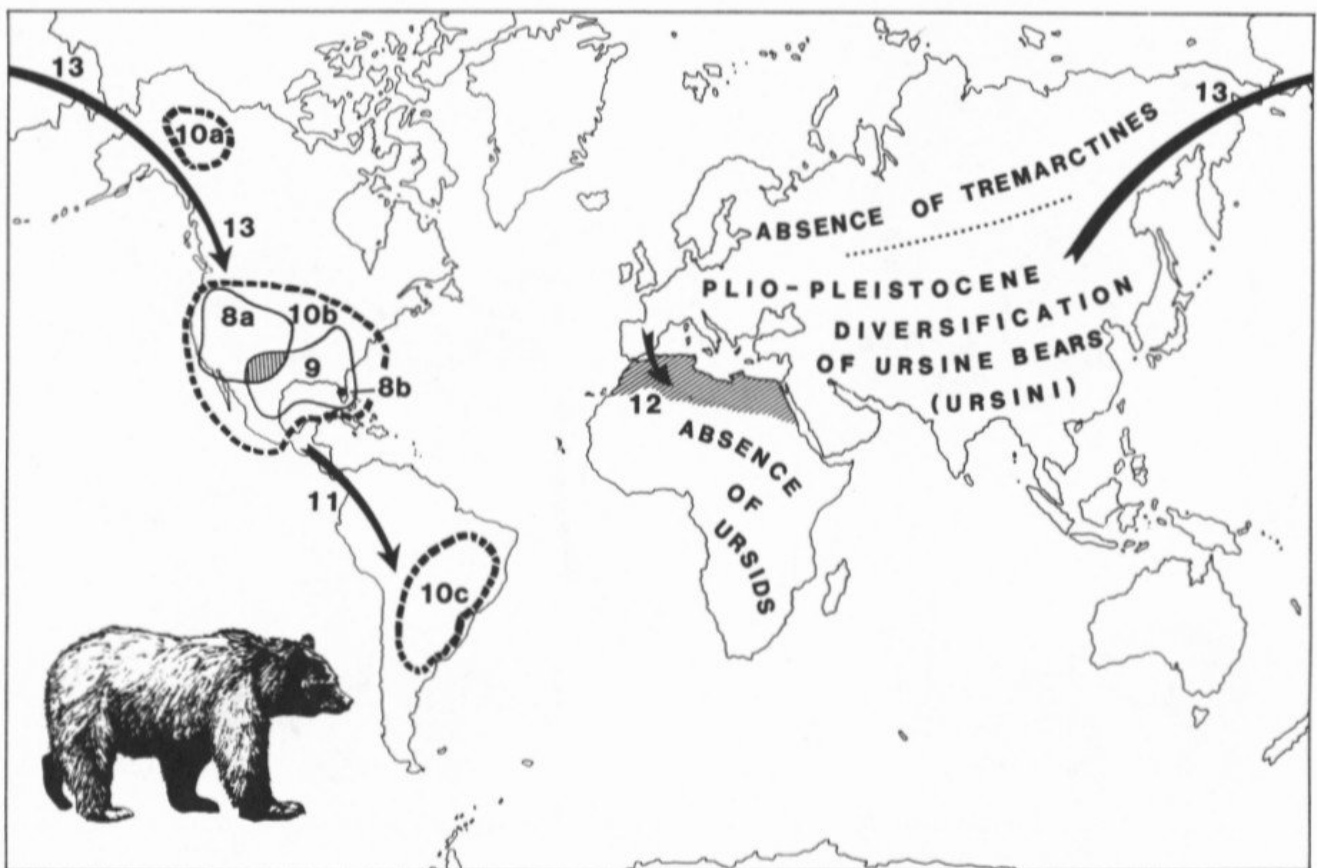


Figure 15.5. Geographic distribution of late Miocene, Pliocene, and Pleistocene ursids (Ursinae: Tremarctini, Ursini). 8, late Miocene and Pliocene *Plionarctos* and *Tremarctos*: 8a, western United States; 8b, Florida (*Plionarctos* only). 9, Pleistocene *Tremarctos*, southeastern United States and Mexico. 10, Pleistocene *Arctodus*: 10a, Alaskan *Arctodus*; 10b, North America (*Arctodus simus-pristinus*); 10c, South America (*Arctodus bonariensis-brasiliensis*). 11, migration of *Arctodus* to South America about 2 Ma. 12, Pleistocene migration of *Ursus* to north Africa. 13, Pliocene migration of *Ursus* to North America about 4.3 Ma.

Miocene Rattlesnake fauna of Oregon. No postcranials of the rare *Plionarctos* are known, but Pleistocene discoveries of short-footed *Tremarctos* and long-footed *Arctodus* demonstrate that these are plantigrade bears (Kurtén 1966, 1967). Kurtén believed that the Tremarctini never evolved the turning-in of the forefeet seen in the gait of the living Ursini.

In North America *Tremarctos* is first known at ~ 2.5 Ma (Opdyke et al. 1977) in the Vallecito (California) and Grand View (Idaho) faunas, and is last recorded at 7000–8000 B.P. in the Holocene Devil's Den fauna, Florida (Kurtén and Anderson 1980).

Arctodus and *Tremarctos* are the only ursids to reach South America. Whereas *Arctodus* possesses a fossil record derived from the Argentine pampas and Brazilian caves, *Tremarctos* is known only from the presence of the living spectacled bear *T. ornatus* in the mountainous regions of northwest South America, extending once perhaps as far south as northern Argentina (Nowak 1991).

Bears of the genus *Arctodus*, at 250–630 kg the largest land carnivorans that ever lived (Kurtén 1967), do not appear in North America until Pleistocene (Irvingtonian) time, and are last known at $12,770 \pm 900$ B.P. (Wyoming) and $12,650 \pm 350$ B.P. (Texas) (Kurtén and Anderson 1980). The great arctodons ranged over all of North America, eventually migrating through Central America to reach South America no earlier than 1.9–2.0 Ma (Marshall 1985:77). The South American arctodons are considered to belong to at least two species, on the basis of dental traits and a marked size difference between the Brazilian and Argentine samples (Kurtén 1967): the largest form, *A. bonariensis*, rivals in size the large North American *Arctodus simus*, but *A. brasiliensis* from Brazil, only somewhat larger than the living spectacled bear, is the smallest known arctodont. Why the tremarctine bears were able to penetrate South America but the species of *Ursus* failed to do so remains an enigma.

Procyonidae

The Procyonidae are usually defined as a New World family of five to six genera (*Bassariscus*, *Bassaricyon*, *Nasua*, *Potos*, *Procyon*) of living arctoid carnivorans that favor forested environments, with all members capable of or strongly inclined toward an arboreal life style. Body size rarely exceeds 15 kg, and the living species (except *Nasua*) are chiefly nocturnal. Most procyonids live in southern North America or in warmer Central and South American subtropical to tropical habitats, with only one genus, *Procyon* (the raccoons), occurring in more northern temperate regions. Despite diverse dentitions and varied appearance, karyotypic uniformity of the living New World procyonids argues that they are a closely related arctoid group (Wurster and Benirschke 1968).

Following Hough's (1948) and Beaumont's (1968) identification of pro-

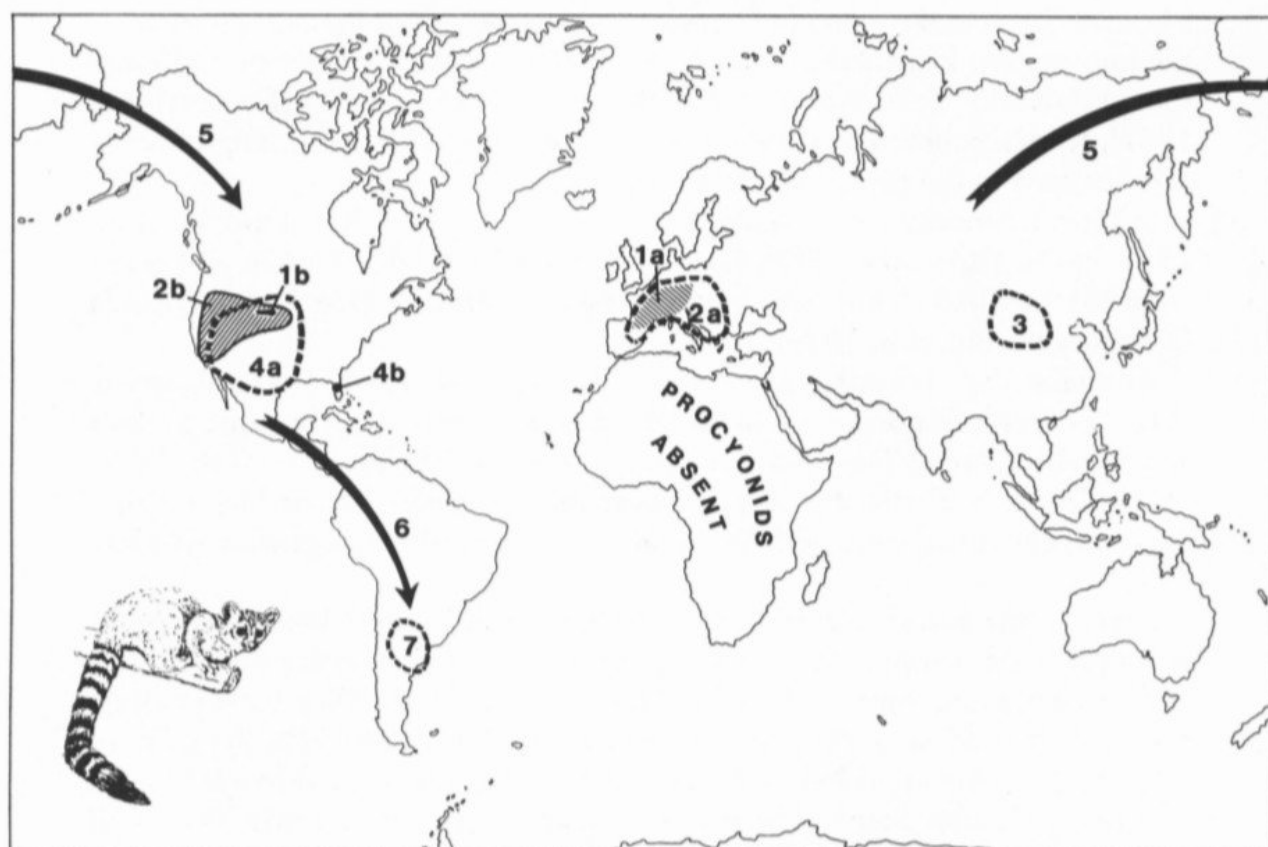


Figure 15.6. Geographic distribution of Oligocene to Pliocene fossil procyonids. 1, Oligocene to early Miocene procyonids: 1a, western Europe (*Amphictis*, *Broiliana*, *Stromeriella*, *Plesictis*); 1b, North America, early Miocene only (*Zodiolestes*, *Stromeriella*). 2, Simocyonines: 2a, Europe, middle to late Miocene (*Alopecocyon*, *Simocyon*); 2b, North America, late Miocene (*Alopecocyon*, *Simocyon*). 3, Simocyonines, middle to late Miocene, north China and Mongolia. 4, early to late Miocene and Pliocene procyonine and bassariscine procyonids: 4a, western United States; 4b, Florida (procyonines only). 5, migration of stem procyonids in early Miocene and simocyonines in middle or late Miocene to North America. 6, late Miocene migration of *Cyonasua*-group procyonids to South America about 7 Ma. 7, late Miocene and Pliocene procyonids, Argentina (*Cyonasua*, *Chapalmalania*).

cyonid basicranial structure in several genera of small arctoids from the latest Oligocene and early Miocene of Europe, it was realized that the family might have been originally Holarctic in distribution (Figure 15.6). Hough and Beaumont recognized three principal European genera with procyonid auditory regions: *Plesictis*, latest Oligocene, Peu Blanc, France, including the genoholotypic species, *P. genettoides*, and *Broiliana* and *Stromeriella*, early Miocene, Wintershof-West, Bavaria. But it has been difficult to segregate these genera morphologically from a plethora of other small European arctoids that radiated in the Oligocene and Miocene (Schmidt-Kittler 1981). Hough's concept of the procyonid auditory region was based upon the living New World procyonids, in which a suprameatal fossa is conspicuously developed. This fossa was central to Hough's (1944, 1948) procyonid concept. In addition, the auditory bulla was a slightly to strongly inflated flask-shaped structure with a

laterally directed bony meatus covering a broad, low petrosal promontorium (in many living mustelids the bony meatus is directed anterolaterally and the promontorium is small, narrow, and constricted by the encroaching bulla margins). The bulla of living procyonids is single-chambered and built from an ectotympanic, a single medially placed caudal entotympanic, and a small rostral entotympanic (Hunt 1974a). When Hough (1948) first recognized a procyonid auditory region in a European carnivoran, the small *Plesictis* from Peu Blanc, it was the suprameatal fossa, the shape and orientation of the bulla and its bony external meatus, the form of the promontorium, carotid canal, and tensor tympani fossa, and the path of the facial nerve that influenced her identification.

In living procyonids the suprameatal fossa lies in the squamosal bone and penetrates both upward into the roof of the external auditory meatus and backward into the mastoid process. It is broadly open ventrally, and among living carnivorans it is developed in this way only in procyonids. The fossa went unnoticed in early studies of the carnivoran auditory region (Turner 1848; Flower 1869) and was not mentioned in Pocock's (1929) investigation of the procyonid auditory region. It first received attention through anatomical dissections of living and fossil carnivorans carried out by Segall (1943) and Hough (1944, 1948) at the Field Museum, Chicago. A hint of the complexity of the fossa was present in Segall's initial work and in later observations by Lavocat (1951, 1952), who observed it not only in living procyonids but also in certain mustelids. Segall explicitly regarded the fossa of procyonids and a similar cavity in mustelids as homologues. Most recently, Schmidt-Kittler (1981) has shown that a suprameatal fossa is widely distributed among arctoid carnivorans: it is rudimentary in many arctoid lineages, never developing beyond a preliminary stage in ursids and ailurids but evolving into a complex feature in procyonids and mustelids.

A ventrally open suprameatal fossa, considered the primitive state by Schmidt-Kittler, occurs not only in a number of Oligocene and Miocene European arctoids but in living procyonids as well. It was presumably floored in these fossil arctoids by a thin connective-tissue membrane like that found in the living *Procyon*. The fossa in raccoons dissected by myself and Matt Joeckel is an empty, air-filled space lined by a thin periosteal covering. The membrane, which is in continuity with the tympanum, is flaccid and distensible. Injection of air or fluid into the fossa distends the membrane, demonstrating that it can protrude freely into the meatus. Its function remains an enigma.

The suprameatal fossa of the living mustelids that possess it is differently configured from that of procyonids. The mustelid fossa is floored by bone rather than membrane, hence is usually not visible when one looks into the auditory meatus. Dissection is required to fully reveal the fossa in living mustelids, and Schmidt-Kittler believes it was reduced or lost, or incorporated into surrounding cavities, in many mustelid species. Despite some uncertainty concerning the homology of the fossa in procyonids and mustelids, it seems reasonable to interpret the procyonid type as a primitive state that in some mus-

telid lineages evolves to a closed chamber in which the cavity is floored by bone.

The most important implication of this interpretation is that procyonids are simply plesiomorphic in this feature, and may share it with other early arctoids. Furthermore, primitive mustelids might possess such a ventrally open fossa that then in some mustelid lineages transforms to the closed state. Thus the Mustelidae could include species with both ventrally open and ventrally closed suprameatal fossae. I suggest here that this is a plausible explanation of the contradiction in dental and auditory structure of the small arctoid *Plesictis* that figured so significantly in Hough's early studies, and I reinterpret the biogeographic patterns on the basis of this viewpoint.

Plesictis remains problematical in its affinities because of its "procyonid" auditory structure coupled with a dentition lacking the posterior molars. Living procyonids always retain M1-2/m1-2, with m2 elongate and m3 absent, and so are unlikely to have evolved from *Plesictis*. The oldest arctoid crania in Europe with well-developed suprameatal fossae belong to *Plesictis* from Peul Blanc and Coderet (MP30, latest Oligocene, ~24 Ma). Because these *Plesictis* species all lack M2 and do not have an elongate m2, they are improbable ancestors for all later procyonids. At nearly the same time (latest Oligocene, MP28, Quercy), the oldest procyonid, *Amphictis*, has only a rudimentary fossa but retains M2/m2. Since the procyonid auditory region may in fact be simply a primitive musteloid feature, these early *Plesictis* might reasonably be regarded as early musteloids with plesiomorphic auditory regions. From a plethora of species of *Plesictis* and *Mustelictis*, the diversity of Miocene and younger mustelids may have arisen (on mustelids, see below), but at present we should not rule out the possibility that some true procyonids may have been included in *Plesictis*, on the basis of Beaumont's (1968) basicranial comparisons.

Beaumont (1968) evaluated specimens of early Miocene *Plesictis* from St.-Gerand, France, and skulls of early Miocene *Broiliana* and *Stromeriella* from Wintershof-West, concluding that they were very similar to *Bassariscus* and the living procyonids in auditory structure. Early Miocene fissure fillings at Wintershof-West, Bavaria (~18 Ma), have produced the best samples of a diverse procyonid ancestral stock, placed by Dehm (1950) in three genera: *Broiliana*, *Stromeriella*, and *Amphictis*. Other, less well-sampled arctoids in the fissures may also belong to this stem group.

The New World procyonids are most likely derived from these Wintershof genera and their earlier European ancestry. All possess an elongate, similarly configured m2, retain M2, and have lost m3, the key dental traits of New World procyonids. *Broiliana* and *Stromeriella* range in the early Miocene from ~18 Ma at Wintershof-West (MN3b) to ~20.5 Ma at Laugnac (MN2b: Bonis and Guinot 1987). They appear to evolve from *Amphictis*, a plausible stem procyonid, which is known from the earliest Miocene to late Oligocene. The cranium of *Amphictis* is known from a single specimen from Quercy (MP28, Pech du Fraysse: Cirot and Bonis 1993), and its auditory region displays many

procyonid features. Because this *Amphictis* skull shows a rudimentary supra-meatal fossa and the Wintershof *Broiliana* and *Stromeriella* have well-developed ones, the fossa appears to have developed in the early Miocene *Amphictis*.

The New World procyonid radiation probably stems from one or at most a very few species of small Eurasian immigrant procyonids that reached North America in the early Miocene. These immigrants retained the ventrally open suprameatal fossa, elongate m2, and M2. Derivation from one or two immigrant species would explain the strong karyotypic identity of the New World forms.

Paleontological evidence from North American fossils provides additional perspective on the origin of the New World procyonids. First, the living and extinct North and South American procyonines *Nasua*, *Procyon*, *Edaphocyon*, *Arctonasua*, *Paranasua*, and *Cyonasua* are the product of a New World radiation first recognized in the early Miocene and identified by derived dental traits emphasizing a hypocarnivorous feeding mode like that found in the living raccoon, *Procyon lotor*, and coati, *Nasua nasua* (Baskin 1982, 1989). Second, the New World ring-tailed cat, *Bassariscus astutus*, retains a more plesiomorphic hypercarnivorous procyonid dentition than do these procyonines, and its teeth and auditory regions are derivable from Oligocene or early Miocene Old World procyonids such as *Amphictis* or *Broiliana*. Bassariscine procyonids (*Bassariscus*, *Probassariscus*) stand apart from the hypocarnivorous procyonines as a distinct lineage first identified in North America in the middle and late Miocene (Baskin 1989).

The procyonines and bassariscines first appear in North America at ~16–18 Ma and are most likely derived from immigrants belonging to the *Broiliana*-*Amphictis*-*Stromeriella* group that existed in Europe ~18–26 Ma. The only record of these genera in the New World is a mandible of *Stromeriella* (or a closely allied taxon) from the early Miocene Runningwater Formation of western Nebraska. The oldest New World procyonine, *Edaphocyon*, also comes from the Runningwater Formation; hence the presence of at least two procyonid lineages in the early Miocene of North America at ~18 Ma provides the earliest evidence of procyonid diversity after the arrival of the family in the New World.

From the New World procyonines, possibly from the Nearctic *Arctonasua* or Holarctic *Stromeriella*, evolve the early procyonid immigrants into South America (Baskin 1982), the *Cyonasua* group (*Cyonasua*, *Chapalmalania*), which first appears on that continent ~7 Ma and extends to ~2.5 Ma (Marshall 1985).

The principal Eurasian group that evolved from these early procyonids is the Simocyoninae (*Alopecocyon*, *Simocyon*). Originally believed by Simpson (1945) to be canids, they are clearly identifiable, on the basis of both dental and basicranial structure, as arctoids, and were claimed as procyonids by Beaumont (1968). The two genera, *Alopecocyon* and *Simocyon*, are Holarctic parallels to canids in their dentition. Both are present in Europe, Asia, and

North America, never diversifying, and become extinct by the end of the Miocene. Simocyonines have an elongate m2, but the hypoconulid is not developed; M2 is not lost or even strongly reduced; the P4 protocone is reduced, retracted; and metaconules are present on the caniform upper molars, but not emphasized. The small arctoid *Amphictis*, with a rudimentary suprameatal fossa, seems likely to be the ancestral simocyonine (the fossa is not strongly developed in the subfamily). Simocyonines and procyonines share the loss of m3 coupled with an elongate m2 talonid and the retention of M2 and a persistent metaconule on M1.

Current consensus favors a relationship between procyonids and mustelids, as either Mustelida (Tedford 1976) or Musteloidea (Schmidt-Kittler 1981). But other than the loss of m3 in both groups and the tendency to develop an elaborate suprameatal fossa in the auditory region (characters that could have developed in parallel), few reliable derived traits unite them relative to an ursid-procyonid dichotomy. The pronounced similarity of the basicranium, bulla, teeth, and skull form shared by early procyonids (*Broiliana* and *Amphictis*) and amphicyonodont ursids (*Amphicyonodon*) supports an ursid-procyonid relationship (see Wyss and Flynn 1993).

The migration of procyonids from Holarctica into the southern continents is a very limited affair. The Old World groups herein attributed to Procyonidae have no record of migration into Africa or southeastern Asia and are restricted to the Eurasian mainland. In South America, however, there are two separate migration events: (1) the invasion of the *Cyonasua* group about 7 Ma (*Cyonasua* is the first placental carnivoran to reach South America: Marshall 1985; Berta 1988); and (2) the later invasion of modern procyonine genera (*Procyon*, *Nasua*, *Potos*, *Bassaricyon*). These living genera are occupants of woodland and forested environments, and it is no surprise that a fossil record is lacking; dating their movement into South America is problematic. Dispersal may have occurred from Central America, beginning at ~2.4 Ma upon completion of the Panamanian land bridge (Marshall and Sempere 1993), and plausibly continued to the present; Pleistocene dispersal is often regarded as probable (Marshall 1985).

Amphicyonidae

The amphicyonids, or beardedogs, are first recognized in the late Eocene of North America, Europe, and Asia. One of the earliest arctoid groups, they are Holarctic in distribution from the time of their appearance in the fossil record (Figure 15.7). They are the first arctoids to reach large body size, and may in fact be the sister group to all other caniform carnivorans.

Alone among arctoids, the beardedogs primitively retain the full eutherian dentition, 3-1-4-3/3-1-4-3. Although the upper molars are reduced in number to two in several lineages (temnocyonines, *Ischyrocyon*, and terminal species

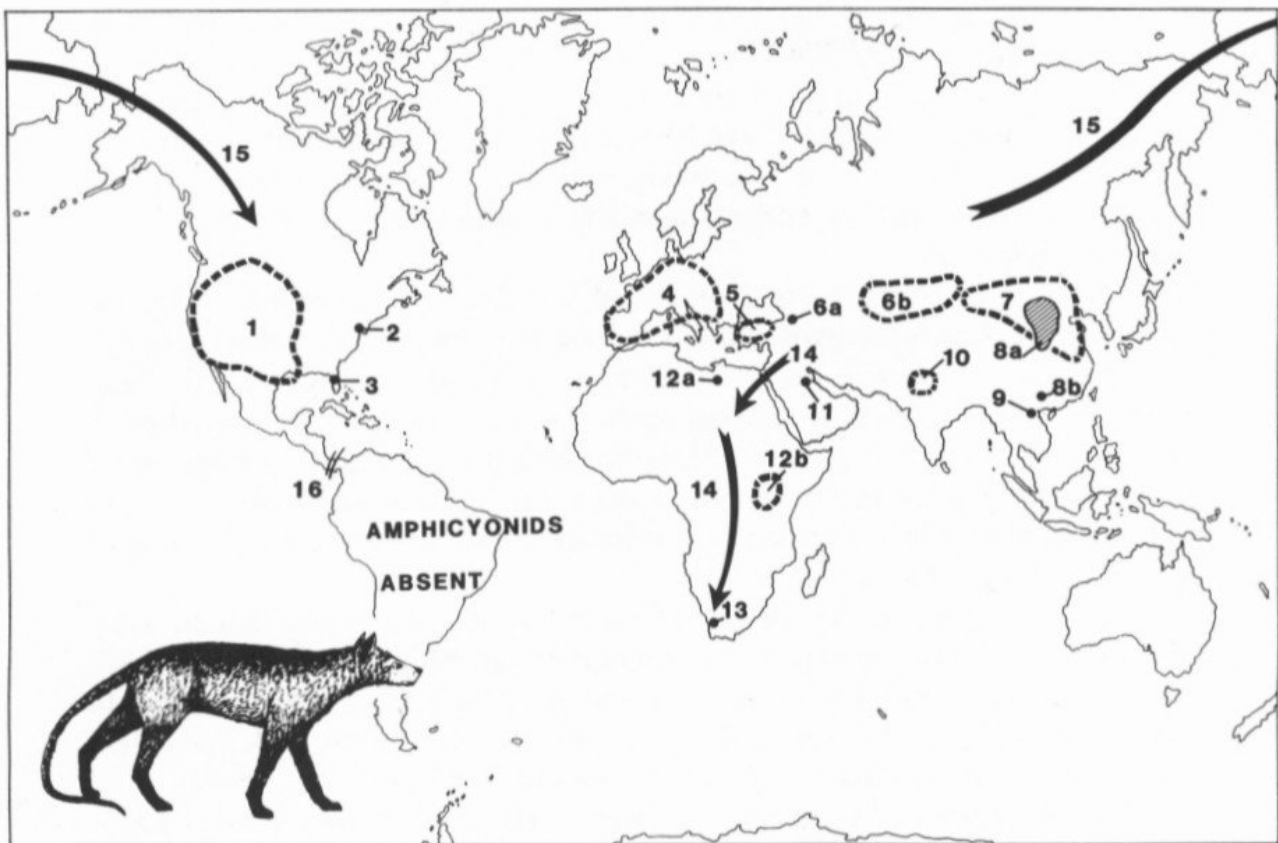


Figure 15.7. Geographic distribution of late Eocene to late Miocene fossil amphicyonids. 1, western North America, late Eocene to late Miocene. 2, eastern United States (Calvert Formation), middle Miocene. 3, Florida, Oligocene and Miocene. 4, Europe, late Eocene to late Miocene. 5, Turkey, middle Miocene. 6, Oligocene amphicyonids: 6a, Georgia; 6b, Kazakhstan. 7, north-eastern China, middle Miocene. 8, Eocene and Oligocene amphicyonids: 8a, north China; 8b, south China (Guangxi). 9, North Vietnam, early Miocene (*Amphicyon*). 10, Siwalik Group, middle to late Miocene. 11, Saudi Arabia, early Miocene. 12, Africa, early Miocene amphicyonids: 12a, Libya (Gebel Zelten); 12b, Kenya. 13, Arrisdrift, Namibia, middle Miocene (including *Amphicyon*). 14, early Miocene migration of amphicyonids into Africa. 15, early Miocene migration of *Cynelos-Ysengrinia* to North America about 19–20 Ma and *Amphicyon* at about 18 Ma. 16, probable southern limit of amphicyonids in the Americas, based on the early Miocene Cucuracha fauna, Panama.

of *Daphoenodon*), the plesiomorphic condition for the family (three upper molars) is preserved in many genera (*Amphicyon*, *Cynelos*, *Daphoenus*, early *Daphoenodon*, *Ysengrinia*) into the early and middle Miocene.

Early beardogs also display the most plesiomorphic condition of the arctoid auditory bulla: the ectotympanic is an unspecialized, unexpanded, simple bony crescent in late Eocene and Oligocene *Daphoenus* (North America) and *Cynodictis* (Europe). No ossified entotympanic(s) occur, but a space between the petrosal and the inner rim of ectotympanic is almost certainly the locus for an entotympanic element (possibly hyaline cartilage or a fibrous connective tissue). Some late Oligocene beardogs have expanded the ectotympanic into a wide, shallow, bony crescent, still quite rudimentary in construction, lacking any ossified entotympanic contribution. By the early Miocene, several beardog

lineages in Europe (*Cynelos*) and North America (*Daphoenodon*) have developed an auditory bulla that completely encloses the middle-ear cavity, comprising fully ossified and fused ectotympanic and entotympanic elements.

Despite the fact that the bulla of Miocene amphicyonids is nearly identical in form and construction to that of ursids, it must have evolved independently in the two families, since the earliest members of both display bullae at different stages of evolution.

In North America the fossil record of beardedogs is unexcelled. Complete skeletons and crania of many genera record a rich diversity that also existed in Europe and, presumably, in Asia. Unfortunately, the European and Asian fossils are often limited to isolated teeth, jaw fragments, and scattered postcrania. But even this sparse evidence demonstrates that many lineages were anatomically similar in dental and postcranial features to North American taxa, indicating a broad Holarctic continuity during the Miocene, the time of greatest diversity for the family.

Beardedogs do not survive the end of the Miocene in Holarctic faunas. They are extinct in North America by the end of the Clarendonian land-mammal age (~9 Ma). In Europe the last known amphicyonid comes from Kohfidisch, Austria, MN11, basal Turolian (Fejfar 1989) or MN10, latest Vallesian (Mein 1989), and is also dated at ~9 Ma (Beaumont 1984). Beardedogs persist until ~7.4 Ma in southern Asia as relicts in Siwalik faunas of Pakistan (Barry 1985; Barry et al. 1982:112; Barry and Flynn 1989), and in the Miocene they penetrate into Southeast Asia as far as northern Vietnam (Hangmon site: Ginsburg et al. 1992). They are unknown in China after the Tunggurian (no amphicyonids younger than 13 Ma are known in eastern Asia).

Beardedogs first appear on the African continent in the early Miocene of the Kenyan rift (*Cynelos*: Savage 1965; Schmidt-Kittler 1987), in Libya (Gebel Zelten: Tchernov et al. 1987), and in Saudi Arabia (Al Sarrar: Thomas et al. 1982; Whybrow 1987), and are among the first placental carnivores to enter Africa from Eurasia. The youngest African occurrence of an amphicyonid, represented by a large, robust rostrum, is from about the middle of the Ngorora Formation, Kenya, and is estimated to be ~11.2 Ma in age (early late Miocene: Barry 1987, pers. comm.; Hill et al. 1985, table 3, *Pseudocyon*[?]). Several amphicyonid lineages are present in Africa during the Miocene, and at least two genera reached South Africa (Namibia), where the great bearlike *Amphicyon* itself has been found in the Arrisdrift fluvial gravels together with middle Miocene ungulates, proboscideans, hyracoids, rodents, and insectivores (Corvinus and Hendey 1978; Hendey 1978).

The biogeography of Holarctic amphicyonids reflects a degree of endemism in the late Eocene and Oligocene followed by evidence of European-North American faunal connections in the Miocene. In the former instance, the late Eocene and Oligocene genera of amphicyonids from the White River beds of North America and from the Quercy fissures of France are distinct lineages, although a familial relationship is evident. Diversity seems greater at Quercy, and several lineages present there continue into the European Miocene. Some

of these European genera suddenly appear as immigrants in North America during the early Miocene, suggesting that European amphicyonids spread rapidly across Eurasia, becoming a key element in the Holarctic carnivoran fauna of the early and middle Miocene.

No amphicyonids ever reached South America, probably due to the absence of a land connection in the Miocene when they, together with the hemicyonine ursids and borophagine canids, were the dominant, large terrestrial carnivorans of North America. Today, the southernmost occurrences of New World amphicyonids are found in the southwestern United States and in Florida. An amphicyonid was recorded in Miocene rocks from Honduras by Olson and McGrew (1941; also Patterson and Pascual 1972: table 2), but later study of these fossils (an essentially edentulous mandible, a partial upper molar, and postcranials) has shown that they belong to the canid *Osteoborus* (Webb and Perrigo 1984). However, a Miocene terrestrial mammal fauna of undoubted northern aspect occurs as far south as Panama in the Cucaracha Formation (Whitmore and Stewart 1965). The scarcity of fossil mammals in the Cucaracha assemblage, together with the fact that only ungulates have been found so far, leaves us ignorant of the carnivore component of the fauna. In North America, however, such faunas are commonly accompanied by diverse amphicyonids. Thus the eventual discovery of beardogs in Central America is plausible and, on the basis of the ungulate component of the Cucaracha fauna, to be expected. The Cucaracha Formation mammals of Panama would seem to indicate the approximate southern limit of penetration for large North American land carnivorans before the completion of the Panamanian land bridge in the late Cenozoic.

Mustelidae

Mustelids rank as the most successful of the small predatory Carnivora. Arising in Holarctica as very small animals ($\sim 1\text{--}2$ kg), the mustelids have never evolved species of large body size (>100 kg), nor do they ever evolve as cursorial open-country predators. Yet they dominate the more densely vegetated habitats, where they occur in both terrestrial and arboreal settings. Today, 23 genera and about 65 species occur throughout the Holarctic, Neotropical, and African regions.

The first mustelids appear in the late Eocene to Oligocene of Europe (*Mustelictis*, Quercy) and North America (*Mustelavus*, South Dakota), but little species diversity is in evidence (Figure 15.8). Diverse mustelids are evident for the first time in the early Miocene of Europe and North America. European (Aquitanian) and North American (late Arikareean) deposits contain multiple lineages that are highly endemic yet broadly comparable in stage of cranial and skeletal evolution. In North America the stem mustelids (*paleomustelids*) of the early Miocene (*Promartes*, *Oligobunis*, *Megalictis*, *Brachypsalis*) represent the first New World mustelid radiation, ranging from small forms less than

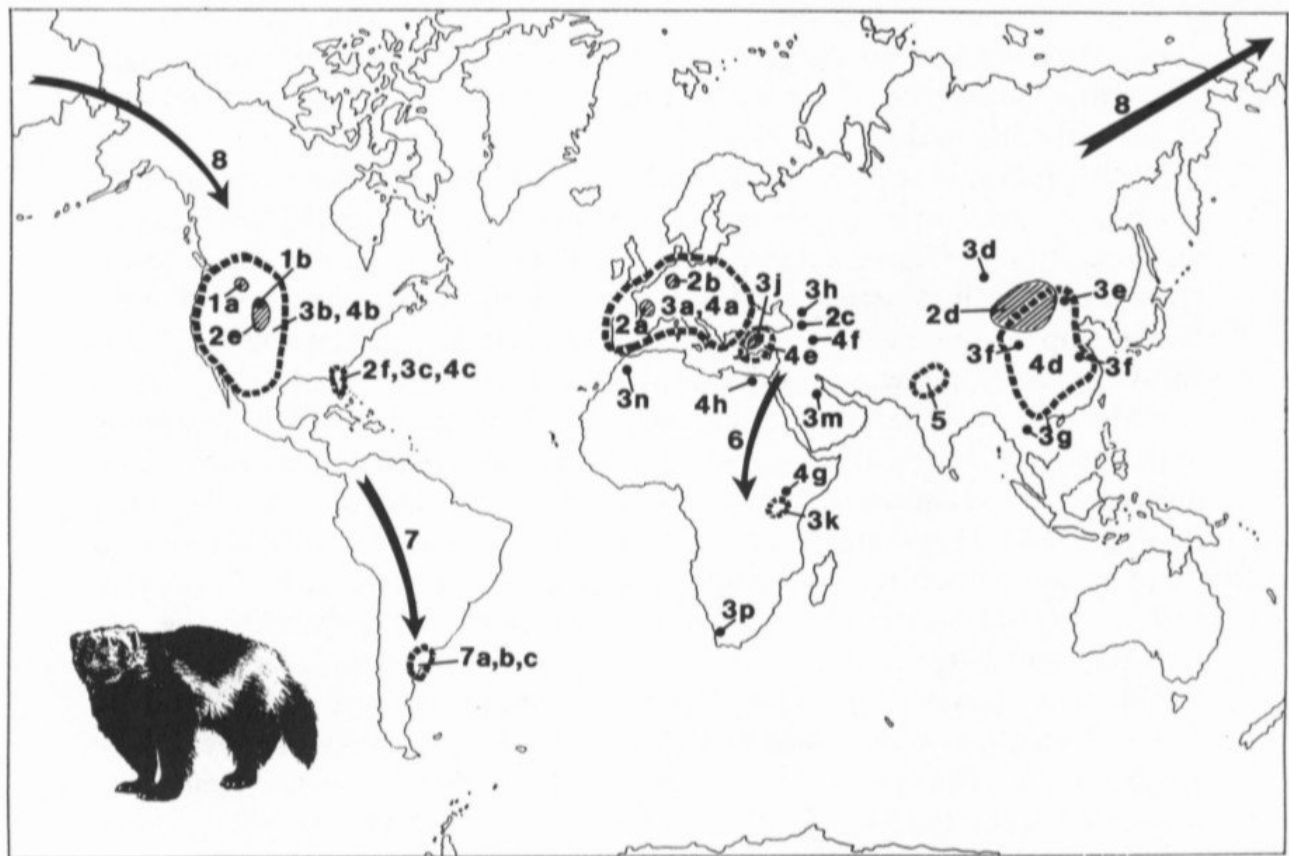


Figure 15.8. Geographic distribution of late Eocene, Oligocene, and Miocene fossil mustelids. 1, late Eocene: 1a, southwestern Montana (Chadronian, *Palaeogale*); 1b, southwestern South Dakota (Chadronian, *Mustelavus*). 2, Oligocene: 2a, western Europe (Quercy: *Mustelictis*, *Plesictis*, *Palaeogale*, ?*Stenogale*); 2b, western Europe (Mainz Basin: cf. *Plesictis*, mustelids); 2c, Georgia (Benara: *Plesictis*); 2d, Mongolia and north China (*Plesictis*, *Palaeogale*); 2e, western North America (White River and Arikaree Groups: *Mustelavus*, *Palaeogale*; 2f, north Florida (I-75 fauna: ?*Palaeogale*). 3, early and middle Miocene: 3a, Europe (early Miocene, MN1–3: *Plesictis*, *Plesiogale*, *Paragale*, *Palaeogale*, *Martes*, *Dehmictis*, *Miomephitis*; MN4: *Martes*, *Palaeogale*, *Mionictis*, *Trochictis*, *Iberictis*, *Ischyriactis*, *Hopliactis*); (middle Miocene, MN5–8: *Mionictis*, *Trochictis*, *Ischyriactis*, *Hopliactis*, *Martes*, *Taxodon*, *Trocharion*, *Trochotherium*, *Proputorius*, *Paralutra*, *Palaeomeles*, ?*Heterictis*); 3b, western North America (early Miocene: *Promartes*, *Oligobunus*, *Megalictis*, *Brachypsalis*, *Palaeogale*, *Leptarctus*, *Craterogale*, musteline n. gen.; middle Miocene: *Mionictis*, *Brachypsalis*, *Martes*, *Miomustela*, *Leptarctus*, *Sthenictis*, *Plionictis*, *Dinogale*; 3c, Florida (earliest Miocene or late Oligocene: *Megalictis frazieri*, SB-1A; indet. Mustelidae, Buda; early Miocene: *Leptarctus*, ?*Oligobunus*; middle Miocene: *Leptarctus*; 3d, northwest China (early Miocene: *Suansuoquan*, *Palaeogale*); 3e, northeast China (middle Miocene: *Tung-Gur*, *Martes*, *Mionictis*, *Melodon*, *Leptarctus*); 3f, north China (early Miocene: *Xie-Jia*, *Sihong*, mustelids); 3g, Thailand (?middle Miocene: *Siamogale*); 3h, Georgia (middle Miocene: *Belometcheskaya*, melliivorine, eumustelid); 3j, Turkey (middle Miocene: *Proputorius*, *Trochictis*, *Hopliactis*, *Anatolictis*, *Plesiogulo*, lutrine); 3k, Kenya (early Miocene: *Luogale*, *Kenyalutra*); 3m, Saudi Arabia (early Miocene: *Mionictis*, cf. *Martes*); 3n, Morocco (middle Miocene: *Beni Mellal*, *Martes*, *Mellalictis*); 3p, Namibia (middle Miocene: *Arrisdrift*, cf. *Ischyriactis*). 4, late Miocene: 4a, Europe (*Martes*, *Ischyriactis*, *Sabadellictis*, *Circamustela*, *Marcetia*, *Mesomephitis*, *Promephitis*, *Trochictis*, *Trocharion*, *Baranogale*, *Paralutra*, *Limnonyx*, *Sivaonyx*, *Enhydriodon*, *Sinictis*, *Promeles*, *Plesiomeles*, *Taxodon*, *Eomellivora*, *Plesiogulo*; 4b, western United States and northern Mexico (*Pliogale*, *Martinogale*, *Buisnictis*, *Mionictis*, *Pliotaxidea*, *Martes*, *Plionictis*, *Sthenictis*, *Ischyriactis*, *Eomellivora*, *Plesiogulo*, *Lutravus*, *Enhydritherium*, *Cernictis*, *Sminthosinus*); 4c, Florida (*Ischyriactis*, *Plionictis*, *Sthenictis*, *Leptarctus*, *Enhydritherium*); 4d, China (*Proputorius*, *Promephitis*, *Sinictis*, *Mustela*, *Martes*, *Meles*, *Melodon*, *Parataxidea*, *Plesiogulo*, *Eomellivora*, *Lutra*, *Sivaonyx*); 4e, Turkey and Samos (*Promephitis*, *Promeles*, *Eomellivora*, *Parataxidea*); 4f, Iran

5 kg to the largest terrestrial mustelids that ever lived (*Megalictis*, 25–65 kg: Hunt and Skolnick, in press). These genera possess mustelid auditory regions but lack important derived features of the upper carnassial (slitlike notch in shearing blade) and M1 (lingual expansion) that distinguish the living species. North American paleomustelids lack a developed suprameatal fossa. The early Miocene European genera (*Plesiogale*, *Paragale*) with mustelid auditory regions also retain the plesiomorphic M1 seen in the North American radiation, but precociously develop the modern upper carnassial (Petter 1967; Schmidt-Kittler 1981), the earliest mustelids to do so.

Representatives of the living subfamilies, here termed *eumustelids*, first appear in the fossil record in the early Miocene. By that time these small predatory arctoids had already attained considerable diversity. Members of the eumustelid radiation are currently recognized by two key anatomical features (Schmidt-Kittler 1981): a suprameatal fossa in the auditory region, ventrally floored by bone (the plesiomorphic arctoid suprameatal fossa lacks a bony floor), and absence of the slitlike notch in the upper carnassial tooth. Some living mustelids lack a developed suprameatal fossa, but in these forms it is presumed to be secondarily reduced or incorporated into adjacent auditory cavities (Schmidt-Kittler 1981).

The rich carnivoran assemblage from the fissure fills at Wintershof-West, Bavaria, dated at ~18 Ma (MN3b: Dehm 1950; Bonis 1981), is the first in the Old World to include eumustelid auditory regions, upper carnassials, and even the linguallally expanded M1 so characteristic of the living groups. (W. D. Matthew, as early as 1924, accurately observed that “in the Miocene Mustelidae the tendency to broaden the inner half of M1, so characteristic of the later genera, becomes progressively apparent.”) Species of small Wintershof eumustelids attributed by Dehm (1950:65–71) to *Martes* and *Laphyctis*? (= *Dehmictis*: Ginsburg and Morales 1992) show upper carnassial and M1 form like that in living mustelids. Their upper carnassials lack the deep slit between paracone and metastylar blade, and their first upper molars have expanded lingual portions without metaconules or postprotocristae (the well-known “wasp-waisted” M1 of many living mustelids). At least two other early Miocene mustelid lineages (MN4: *Trochictis*, *Iberictis*) also possess linguallally expanded first upper molars (Ginsburg and Morales 1992).

Somewhat prior to this, in the early Miocene Aquitanian deposits at Montaigne-le-Blin, France (MN2a, 22–23 Ma), crania of *Plesiogale* and *Paragale* display eumustelid upper carnassials and auditory bullae configured as in

(*Martes*, *Promeles*, *Parataxidea*); 4g, Kenya (mellivorine, *Vishnuonyx*, *Enhydriodon*); 4h, Wadi Natrun (*Enhydriodon*, *Aonyx*, ?*Topolutra*). 5, Siwalik Group (middle Miocene: *Martes*, *Hoplictis*, *Vishnuonyx*; late Miocene: *Eomellivora*, *Sivaonyx*, cf. *Ischyriactis*, mustelid indet.). 6, early Miocene migration of mustelids to Africa (earliest records at Rusinga and Songhor in Kenya, and As-Sarar, Saudi Arabia). 7, late Pliocene and early Pleistocene migrations of mustelids to South America: 7a, Chapadmalal Fm., ~2.4–2.5 Ma (*Conepatus*); 7b, Vorohue and San Andres Fms., ~1.9–2.4 Ma (*Galictis*, *Stipanicia*); 7c, Ensenadan, ~1.4 Ma (*Lutra*, *Lyncodon*). 8, periodic Miocene migrations of mustelids from Eurasia to North America (*Plesiactis*-group, leptarctines, *Martes*, *Mionictis*, *Ischyriactis*, *Eomellivora*, *Plesiogulo*, and others).

living mustelids (Viret 1929: pl. 13, figs. 4, 5; Beaumont 1968: pl. 1; Petter 1967, pl. 1, fig. 1), but the suprameatal fossa is not yet fully floored ventrally by bone and M1 shows only rudimentary lingual expansion. Thus, in both morphology and placement in time, *Plesiogale* and *Paragale* can be considered as transitional forms between the archaic paleomustelids and the eumustelid radiation. Schmidt-Kittler (1981) designated the Aquitanian species as a *mustelides Fruhstadium*, or early stage, visualizing the living eumustelids as the late stage, or *Hauptstadium*.

In North America the oldest eumustelid is represented by a complete skull with basicranium from the Kimberly Member of the John Day Formation, Oregon (~23 Ma), of earliest Miocene age. The same lineage appears in the late early Miocene Runningwater Formation at Cottonwood Creek Quarry, Dawes County, Nebraska (~18 Ma), where it is represented by a posterior cranium with well-preserved auditory region. This Runningwater cranium is an excellent morphological antecedent stage to a nearly complete skull with basicranium of a small musteline from Observation Quarry, western Nebraska (~16–16.5 Ma). These three crania document an evolving lineage of small mustelines, closely related to *Mustela*, over an interval of about 7 million years in the early Miocene. The fossils demonstrate that by the beginning of the Miocene in North America this eumustelid line had already evolved the enlarged braincase and small rostrum of living *Mustela*. As shown by the basicrania, the specimens also record a remarkable transition from a simple flask-shaped auditory bulla to the elongate and enlarged bulla of living *Mustela* species.

The skull form and basicranial structure of these earliest North American eumustelids are similar to those of the European early Miocene *Plesictis julienei* from Aquitanian deposits at St.-Gerand, France (Viret 1929: pl. XV, fig. 5). Although not identical in cranial morphology, the European and North American fossils are plausibly related, sharing a highly similar configuration of the auditory bulla and surrounding cranial features. The simple flask-shaped bulla of the European *P. julienei* is found in the two earliest eumustelid crania from North America, and it is this type of bulla that becomes progressively modified in the North American fossils during the later early Miocene into the inflated, elongated bulla of *Mustela* seen at Observation Quarry in Nebraska.

In contrast to the European fossil record, the North American record lacks transitional forms between the paleomustelids of the late Arikareean and the first eumustelids of the medial Arikareean–early Hemingfordian age, suggesting that the modern eumustelid subfamilies originated in Eurasia and entered North America as immigrant lineages, beginning in the earliest Miocene and continuing into the middle Miocene. Immigrant eumustelids replaced the North American paleomustelids, which largely became extinct by the end of the early Miocene. The morphological similarity of the oldest skulls of New World eumustelids to skulls of European mustelids like *Plesictis julienei* strongly supports the argument for a common Old World ancestry for these North American eumustelid groups.

Mustelines (weasels, martens, wolverines, badgers), mellivorines (ratels), mephitines (skunks), and lutrines (otters) are all represented as distinct lineages in the Holarctic late Miocene.

A particularly striking feature of all living mustelids is the loss of their posterior molars; they retain only the first molar in the maxilla and the first and second molars in the mandible. The elongate m2 of procyonids does not occur. In fact, the early Miocene European fossils from Montaigu and Wintershof-West have already attained this degree of molar reduction. The loss of M2 in these earliest predecessors of the eumustelid radiation explains the elaborate talon appended to the M1 in many lineages of living mustelids: in order for the m2 in the mandible to maintain contact with a tooth in the maxilla, the M1 must grow backward by developing an elaborate talon, which then occludes with m2 (commonly only the m2 trigonid contacts M1). Thus the occlusion of the M1 talon with m2 is a neomorphic relationship, a derived trait appearing independently in many eumustelid lineages (some living eumustelids lack M1/m2 occlusion or develop only a rudimentary contact, as for example in *Mustela*). The presence of an M1 talon therefore demonstrates beyond any doubt that at the time of origin of the lineage the second upper molars had already been lost (which implies loss of m3 as well).

In Asia, mustelids of Oligocene and early Miocene age are few and largely undescribed. Accordingly, we know very little about the presence of stem mustelids or eumustelids relative to those of Europe and North America, where the best fossil record occurs. In the most recent summaries of Chinese Neogene mammal faunas, Li, Wu, and Qiu (1984) and Qiu and Qiu (1990) report undetermined mustelids, "*Mustela*," and *Proputorius* from the early Miocene (Xiejia and Sihong faunas); and *Leptarctus*, *Martes*, *Mionictis*, and *Melodon* from the middle Miocene (Tung Gur fauna).

Migration to the southern continents occurred first in Africa in the early Miocene, much later in South America in the Quaternary. The immigration of mustelids out of Holarctica and into Africa is recorded by the presence of a probable lutrine and a stem mustelid (near the European *Paragale*) in the early Miocene of east Africa (Schmidt-Kittler 1987), and also by *Mionictis* and cf. *Martes* from the early Miocene of Saudi Arabia (Thomas et al. 1982). Surprisingly, the oldest African mustelid is reported to be the otter *Kenyalutra* from Songhor (European zone MN3, ~19.6 Ma: Schmidt-Kittler 1987), known only from a specialized lower carnassial and a tooth fragment. This occurrence is followed at Rusinga (MN4, ~17.8 Ma) by a second African mustelid, *Luogale*, known from two maxillary fragments and a partial mandible (Schmidt-Kittler 1987). As in the eumustelids, the P4 of *Luogale* appears to lack the carnassial notch. *Luogale* is more generalized, and appears to be derivable from early Miocene *Paragale-Plesiogale* from the Aquitanian of France, which are much like martens and are the oldest European fossils with the eumustelid P4.

It is difficult to determine if in fact mustelids were as diverse in the African early Miocene as they were in Europe. The occurrence of mustelids in the early

Miocene of Saudi Arabia at the Al Sarrar site (Thomas et al. 1982) suggests that the family may have been widely distributed in northeast and east Africa by this time. Penetration of the family into southern Africa by the middle Miocene (about 15–17 Ma) is evidenced by a carnivorous mellivorine in the Arrisdrift fauna of Namibia (Hendey 1978). A mellivorine is also present in the late Miocene of north Africa (Ginsburg 1977).

Mephitines, mustelines, and lutrines invaded South America from the north, beginning in the Pliocene, ~2.4–2.5 Ma (Chapadmalalan land-mammal age: Marshall et al. 1983; Marshall and Sempere 1993), and continuing into the Pleistocene, and are today represented by 14 species distributed widely over the continent in varied habitats. Eleven of the 14 have been considered endemic (HersHKovitz 1972). Mustelids are among the first carnivoran families of North American origin to enter South America via the Panamanian land bridge: the earliest recorded immigrant is the mephitine *Conepatus* in the Chapadmalalan Formation of Buenos Aires Province, Argentina, where it occurs with the endemic procyonids *Cyonasua* and *Chapalmalania* (Reig 1952; Marshall et al. 1983). Species of *Conepatus* are the only mephitine skunks to reach South America; three living and multiple fossil species are recognized (seven fossil species are known from Argentina, Brazil, Bolivia, and Peru: Berta 1988). In the overlying Vorohue and San Andres formations (Marshall et al. 1984), the endemic weasels *Galictis* and *Stipanicia* appear, followed in the Ensenadan age by the endemic Patagonian weasel *Lyncodon* and the first otters (*Lutra*). In the Lujanian, *Mustela* makes its appearance in South America, where today it is known from three species confined to the northern part of the continent. The martenlike *Eira* and the giant Brazilian otter *Pteronura*, each known from a single species endemic to South America, have no fossil record certainly older than Holocene.

South American mustelid genera with present-day northern congeners include nine species of skunks, otters, and weasels (*Conepatus*, *Lutra*, *Mustela*); southern endemics are represented by three species of weasels (*Galictis*, *Lyncodon*), the martenlike *Eira*, and the giant Brazilian otter *Pteronura*. On the basis of the temporally staggered appearance of various mustelid lineages in the South American fossil record, we can state that mustelid immigration into the continent probably involved a series of pulses distributed over the last 2.5 million years, rather than a single immigration event.

Ailuridae

The fossil record of the red panda (*Ailurus fulgens*) is limited to the late Ruscinian-Early Villafranchian (middle Pliocene, 3–4 Ma) of Europe (Tedford and Gustafson 1977 for localities) and to Pleistocene cave sites in China (Bien and Chia 1938). In North America, a single upper molar has been discovered in early Blancan fluvial sediments of Washington. Dental remains from Europe

(Schmidt-Kittler 1983) and from the Siwaliks of southern Asia (Gingerich and Sahni 1979), referred to *Sivanasua* and once believed to be ancestral ailurids, are now known to belong to feliform Carnivora and primates, respectively. Thus the oldest ailurids are Pliocene.

Ailurids were once Holarctic in their distribution, but today are restricted to mountain forests in Nepal, north Burma, and south China. Known fossils are limited to cranial and dental remains very similar to those features in the living animal; no postcranials are known, but the primitive, arboreally adapted skeleton of *Ailurus* with plantigrade feet has probably not changed since at least the Pliocene.

The red panda (*Ailurus*, *Parailurus*) and giant panda (*Ailuropoda*) have been variously considered as most closely related to procyonids or ursids, or placed in their own families, Ailuridae Flower 1869 and Ailuropodidae Pocock 1921. Basicranial structure and the classic monograph by Davis (1964) establish that the giant panda is an ursid. The nature of the red panda has been more difficult to solve. Attempts to address this question have usually proceeded from a strong focus on, and comparison with, living forms, most often ursids and procyonids. This perspective should be modified, however, in view of the much better fossil record of arctoid Carnivora available since the question of panda origins was first addressed in the nineteenth century. From a paleontological perspective, the red panda is a Eurasian derivative of the early arctoid radiation, and hence has relationships with both ursids (Ginsburg 1982) and procyonids (Gregory 1936; Roberts and Gittleman 1984). Its basicranial anatomy is very similar to that of middle Cenozoic ursids such as *Cephalogale*, but its molar teeth lack the characteristic ursid occlusal pattern, in which the metaconule shifts to the posterointernal corner of the tooth, creating a quadrate molar. *Ailurus* most likely evolved from a dentally plesiomorphic species of amphi cynodont or *Cephalogale* that subsequently developed the elaborate cusping of the cheek teeth characteristic of the living species, *A. fulgens*.

The red panda serves as a particularly instructive example of the value of the fossil record, by emphasizing the fact that present-day family-level groupings of living arctoids (ursids, procyonids, mustelids) do not adequately communicate the known paleontological diversity that characterized the arctoid radiation of the middle to late Cenozoic.

Otariidae-Phocidae-Odobenidae

The pinniped carnivorans (sea lions, seals, walruses) are aquatically adapted arctoids that underwent a major Neogene radiation in the world's oceans. Current evidence suggests that the oldest pinnipeds, the enaliarctines, are derived from terrestrial ursids (Hunt and Barnes 1994; Mitchell and Tedford 1973), and that pinnipeds may be monophyletic (Fay et al. 1967; Wyss 1987). Their biogeography, a subject in its own right, has recently been reviewed by

Repenning et al. (1979). The striking biogeographic separation of otariids in the Pacific and phocids in the Atlantic and Tethyan realms argues for distinct and early origins for the two major groups, plausibly from amphi-cynodont ursids. Unfortunately, the paucity of early phocid skulls with plesiomorphic basicrania hinders our comprehension of phocid origins within the arctoid group. Additional studies presenting relevant biogeographic information include Repenning (1976), Barnes et al. (1985), Mitchell (1975), and Repenning and Tedford (1977).

Biogeography of the Cynoids

Basicranial structure and dental traits indicate that the canids, the only cynoid family, are more closely related to the arctoids than to aeluroids. All living and extinct canids are united by the form and structure of the auditory bulla, its ontogeny (including the development of an *entoseptum* within the bulla), and the path of the internal carotid artery in the auditory region (Hunt 1974a, 1987). In the early ontogeny of living canids the bulla is made up of three separate bony elements: ectotympanic, rostral entotympanic, and caudal entotympanic (Figure 15.1). Initially, the bulla is of little volume, lacking any degree of internal expansion. During ontogeny, however, the caudal entotympanic enlarges relative to the other elements, producing an inflated middle-ear cavity of increased volume in the adult. During this growth process a shelflike bony septum develops within the bulla, largely or exclusively from the inflected margin of the caudal entotympanic (hence the term *entoseptum*). In early canids, the septum appears to have been contributed by the full circumference of the inflected caudal element, whereas in living Caninae the septum is restricted to the anterior part of the bulla (Wang, pers. comm.).

Furthermore, in canids the internal carotid artery enters the basicranium at the posterior lacerate foramen, and travels in a common passageway with the inferior petrosal venous sinus, rather than, as in arctoids, in a separate bony tube (carotid canal) in the medial bulla wall. In the anterointernal corner of the auditory region the artery runs in a short bony tube formed by the rostral entotympanic before entering the cranial cavity (Hunt 1974a). The extrabullar location of the internal carotid relative to the caudal entotympanic, found in all but the earliest canids, is an important derived trait uniting the family.

The canid dental formula is generally 3-1-4-2/3-1-4-3 (except in the African *Otocyon*, where it is M3/4).

In the living Caninae we find evidence of cursorial adaptation, in the lengthening of the lower limb segments and the restriction of limb movement to favor fore-aft motion, with lessened ability to pronate-supinate the forelimbs. The Caninae achieve this high degree of limb specialization by restriction of joint motion, appression of the metapodials and digits, and lengthening of distal limb elements, including tarsus and carpus.

Canids are originally endemic to North America, a fact still unappreciated

by some students of carnivorans, who mistakenly place several Old World canid parallels, particularly certain amphicyonids and hemicyonine ursids, with the true canids. Canids first migrate to the Old World at ~9 Ma, when the first true fossil canid appears in the late Miocene of Spain (Crusafont-Pairo 1950). Shortly thereafter, *Canis*, *Vulpes*, and *Nyctereutes* all occur in the Pliocene of Eurasia.

Canidae

Canids are represented by three successive radiations (hesperocyonine, borophagine, canine) that take place in the Nearctic region during the middle to late Cenozoic (Figure 15.9). From their first appearance in the late Eocene until the late Miocene, the family is exclusive to North America, filling a broad spectrum of omnivorous and carnivorous niches for predators of small to medium body size (<100 kg). Beginning in the late Miocene and continuing into the Plio-Pleistocene, the third radiation (Caninae) spreads over Eurasia (9 Ma), Africa (4–5 Ma), and South America (2 Ma).

The first canid radiation during the late Eocene to early Miocene is distinguished by a diverse array of small canids of the subfamily Hesperocyoninae. The largest species are early Miocene end members of the *Mesocyon* and *Enhydrocyon* lineages, which have body weights of less than 20 kg. Both lineages evolved directly from the stem canid *Hesperocyon* (<3 kg), which is the first and only representative of the family in the late Eocene of North America. Hesperocyonines retain a plesiomorphic triangular M1, bordered by a strong lingual cingulum, that bears conules but lacks the enlarged metaconule of ursids and many procyonids. Most species retain primitive canid dentitions, with the exception of the *Enhydrocyon* line, in which the premolars become robust crushing teeth and the rear molars are reduced, resulting in the first canid parallel to durophagous Old World hyaenids. Only *Hesperocyon* occurs in the late Eocene, but it is joined in the early Oligocene (Brule Formation of the Great Plains) by the somewhat larger *Mesocyon*. During the late Oligocene and early Miocene, hesperocyonine diversity reaches its peak: rocks of that age from the Great Plains and Rocky Mountain basins have produced multiple species of small hesperocyonines.

Borophagine canids, the second canid radiation, evolved from the hesperocyonines in the late Oligocene, stemming from small, fox-sized species of *Tomarctus* and “Nothocyon.” During the Miocene, borophagines increased steadily in size and filled a variety of niches paralleling those of small foxes, coyotes, wolves, omnivorous procyonids, and bone-crushing hyaenids. Among them are large cursorial wolflike (*Aelurodon*) and hyena-like (*Osteoborus*, *Borophagus*) canids that evolved in response to open savanna and grassland environments in the late Miocene and Pliocene. The M1 in borophagines is initially more quadrate than in hesperocyonines, largely as the result of a developed metaconule which, with the lingual cingulum, contributes to the

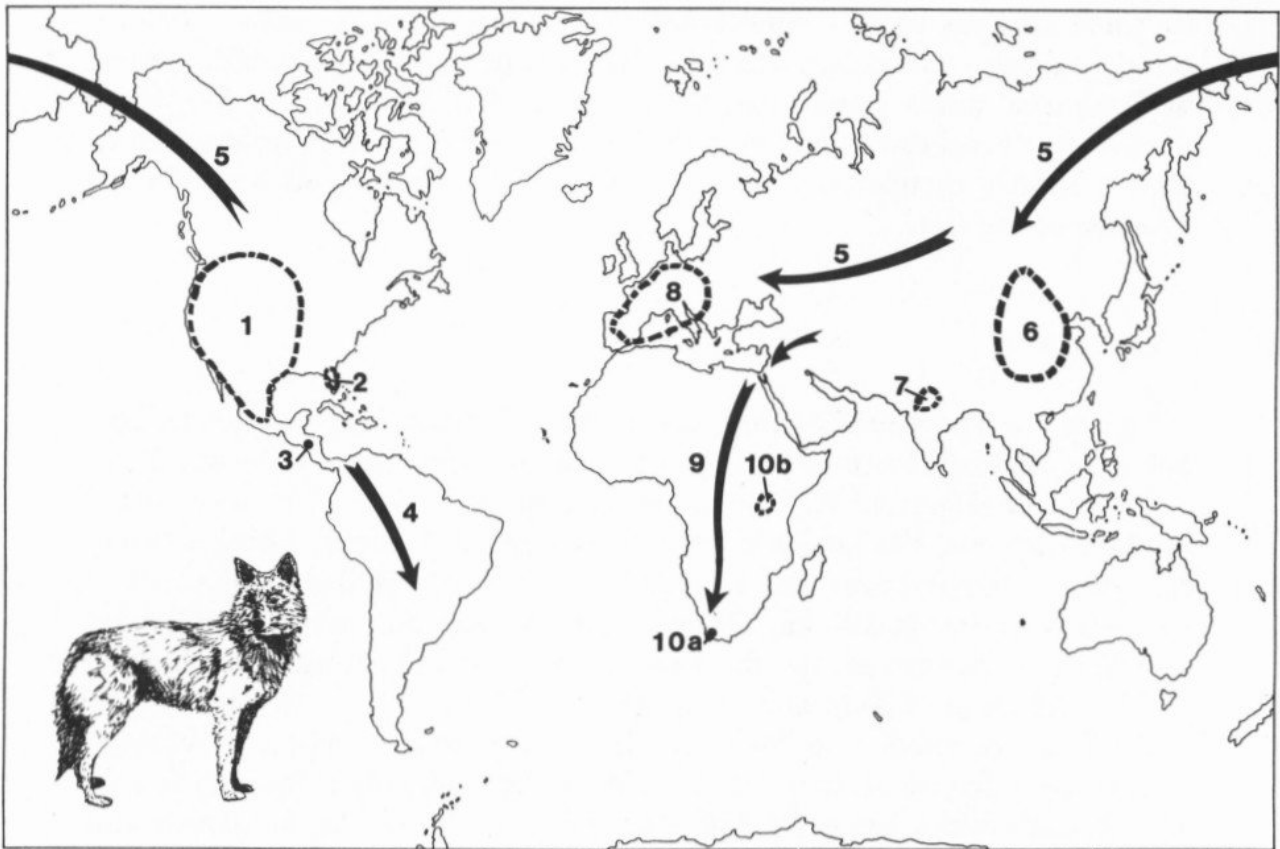


Figure 15.9. Geographic distribution of late Eocene to Pliocene fossil canids. 1, late Eocene to Pliocene, North America (Hesperocyoninae, Borophaginae, Caninae). 2, Oligocene to Pliocene, Florida. 3, southern limit of canids in the New World during the Oligocene and Miocene (Honduras, *Osteoborus*). 4, late Pliocene and Pleistocene migrations of canids (Caninae only) to South America, 1.4 Ma and 2.0–2.4 Ma. 5, late Miocene and Pliocene migrations of canids (Caninae only) to Eurasia, as early as 7 Ma. 6, Pliocene canids, eastern Asia (*Nyctereutes*–“*Canis*,” first appearance about 4–5 Ma; *Vulpes*–*Canis*, about 3 Ma; *Cuon*, about ?2–3 Ma). 7, Pliocene canids, Siwalik Group, first appearing in *Elephas planifrons* interval-zone, about 1.5–2.9 Ma. 8, Europe, late Miocene (“*Canis*” *cipio*, *Nyctereutes*) and Pliocene (*Canis*, *Vulpes*, *Nyctereutes*) canids. 9, early Pliocene migration of canids into Africa about 4–5 Ma. 10, Pliocene canids, Africa: 10a, Langebaanweg (*Vulpes*); 10b, Laetoli (*Cerdocyon*-group and other canids).

quadrate outline of the molar. The radiation terminates with the hyena-parallel *Borophagus* in the Pliocene of North America; no borophagines survive into the Quaternary.

The rich diversity of living canids on all continents reflects the success of the final radiation, the subfamily Caninae. Canines evolve from a single lineage of early cynoids, the small, fox-sized *Leptacyon* of the late Oligocene and early to middle Miocene of North America. The dental pattern in living Caninae does not differ to any significant extent from that of this small carnivore except in tooth size, indicating the remarkably conservative nature of the canine dentition. Diversification of canine canids does not occur until the late Miocene, when *Canis* and *Vulpes* first appear, followed by the principal canine radiation in the Plio-Pleistocene.

Canines are the first canids to enter the Old World (the borophagines and hesperocyonines are restricted to North America), appearing in Europe in the late Miocene (Crusafont-Pairo 1950), and in Africa in the early Pliocene (Langebaanweg: Hendey 1974; Laetoli: Petter 1987; Barry 1987), where at the Tanzanian locality they are already diverse. Canids enter South America in the late Pliocene at ~ 2.0 – 2.4 Ma, with the appearance of *Protocyon* in Argentina (Vorohue Formation, Buenos Aires Province). Three other genera of large canids (*Theriodictis*, *Chrysocyon*, and *Canis*) and the small *Cerdocyon* appear in South America in association with an early Pleistocene dispersal event at ~ 1.4 Ma (Marshall 1985; Berta 1988). All of the large canids, with the exception of *Chrysocyon*, become extinct by the Holocene. In addition to a single species of *Chrysocyon* (the maned wolf, *C. brachyurus*) that survives in central South America, six other genera of living canids are found today in South America (*Urocyon*, *Speothos*, *Atelocynus*, all from northern South America; *Cerdocyon*, northern and central South America; *Pseudalopex*, broadly distributed in South America; *Dusicyon australis*, the Falkland Island fox, extinct about 1876). The South American canids very probably evolved from a few northern immigrant forms of the Caninae that entered the continent soon after land connections were established, and then evolved endemic species adapted to local conditions.

In Africa, *Canis* is represented by three species of jackals with a sub-Saharan distribution, and the gray wolf (*C. lupus*), which penetrated only into northeast Africa. Though it is not found in South America, the fox (*Vulpes*) occurs throughout Africa, and the smallest living canid, *Fennecus zerda*, the fennec fox, occupies northern Africa. The African wild dog (*Lycaon pictus*) and bat-eared fox (*Otocyon megalotis*) are endemic and confined to sub-Saharan Africa. This degree of canine diversity is already evident by ~ 3.5 Ma at Laetoli, in Tanzania.

In the Oligocene and Miocene, canids occupy many niches in North America that are the province of arctoids in the Old World. Eurasia clearly emerges as the staging ground of arctoid evolution, certain lineages spilling over by immigration into North America and Africa. As the sister group to the arctoids, cynoids flourish in North America (and eventually South America as well), occupying arctoid roles for small to mid-sized carnivores and omnivores, but relinquishing the large carnivorous niche (>100 kg) to amphicyonids, ursids, and felids.

Biogeography of the Aeluroids

Aeluroid carnivorans include, as a core group, the families Viverridae, Herpestidae, Felidae, and Hyaenidae (Flower 1869; Hunt and Tedford 1993). The extinct catlike Nimravidae and the Recent Malagasy aeluroids have been the focus of recent research and are also discussed here. Aeluroids are essentially Old World carnivorans: the viverrids, herpestids, and hyaenids are restricted

almost entirely to Eurasia and Africa, the only significant exception being the immigration into North America in the Plio-Pleistocene of a single hyaenid lineage (*Chasmaporthetes*), known only from the southern United States and Mexico. Felids are the only aeluroid family that successfully attains a degree of species diversity in the New World, reaching all of North America and penetrating into South America during the glacial maxima at $\sim 1.9\text{--}2.0$ Ma, when *Felis* and *Smilodon* appear for the first time in company with other carnivorans such as large arctodont bears (Marshall 1985).

Just as for arctoids, the early diversity of aeluroids is first recorded in the Quercy fissure fills of France (late Eocene to Oligocene), where several aeluroid lineages are interpreted to be ancestral stocks of felids and viverrids. The evidence in Asia at this time is very poor, but the principal site yielding aeluroids, Hsanda Gol (Mongolia), provides evidence of lineages similar to, if not the same as, those at Quercy, indicating a probable Palaearctic distribution for these early aeluroids. No aeluroids are known from Africa until ~ 20 Ma in the early Miocene (Schmidt-Kittler 1987; Hunt and Tedford 1993), when multiple lineages of small aeluroid carnivorans occur in the rift sediments of Kenya.

The migration of a single aeluroid family into the New World is an early middle Miocene event: true felids enter North America via Beringia and make their first appearance at $\sim 16\text{--}17$ Ma in the Great Plains (Hunt 1987:3).

Aeluroids are most reliably identified by the uniquely derived morphology of the auditory region (Figure 15.1), particularly the construction of the auditory bulla and the form of the petrosal (Hunt 1987, 1989, 1991; Hunt and Solounias 1991; Hunt and Tedford 1993 and references therein). Important features include the relationship of the caudal entotympanic element of the bulla to the ectotympanic bone, and the development of a ventral promontorial process of the petrosal. Moreover, in contrast to arctoids, each of the aeluroid families is recognized by a distinctive auditory bulla morph and a pattern of ontogenetic development that remains stable over a significant time interval in the middle and late Cenozoic (Figure 15.10).

Among the living Carnivora, the aeluroids alone have developed, in some lineages, elaborate carotid retia in the orbital region for cooling warm arterial blood flowing to the brain (Baker 1979, 1980, 1982; Paule and Baker 1978; Frackowiak 1989; Davis and Story 1943). The aeluroids that attain large body size, the felids and hyaenids, have this countercurrent heat-exchange mechanism. This rete may be a significant factor in the dissipation of body heat in large, exercising carnivorans and in the adaptation of large aeluroids to warm, open environments.

Viverridae

Living viverrids, small to mid-sized (to 20 kg) carnivorans of the Old World tropics, include about 19 genera of chiefly nocturnal (but some diurnal) predators, omnivores, and frugivores, occupying Africa, southern Asia, the East

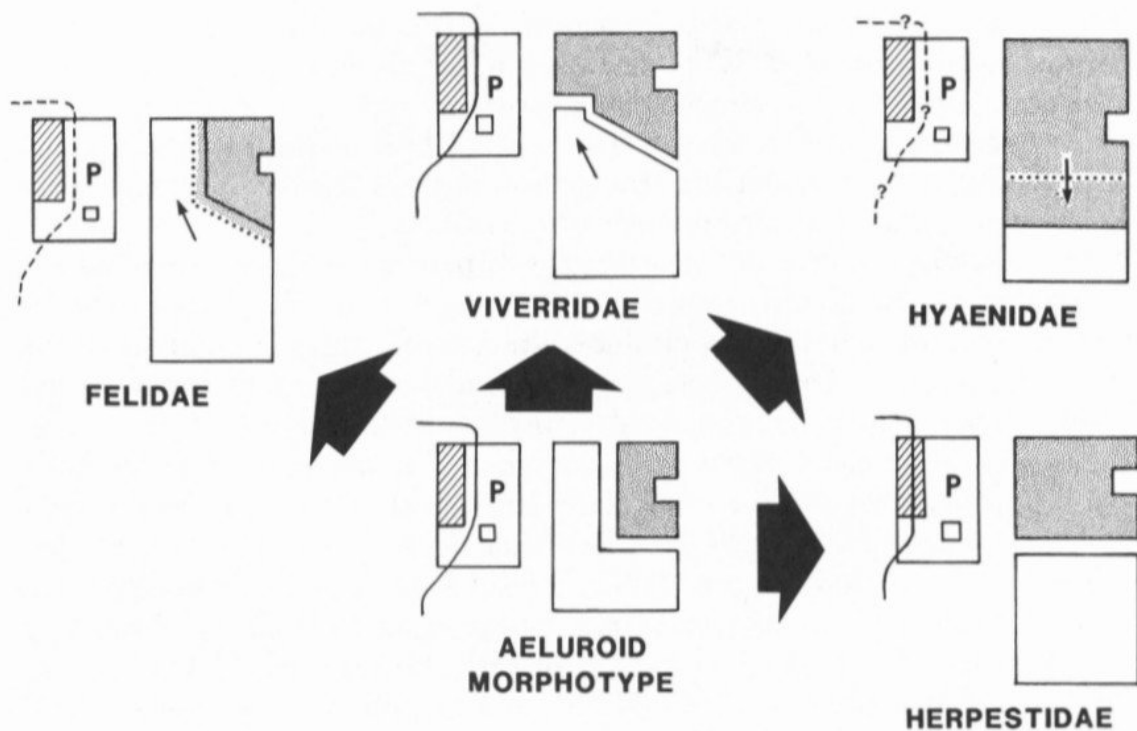


Figure 15.10. Evolution of the auditory bulla in aeluroid carnivorans. The diagrams, which represent the left auditory region in ventral view, anterior to top, illustrate a progression from a morphotype to the derived character states of the living families. The left side of each diagram indicates the relationship of petrosal (P), rostral entotympanic (hatched), and internal carotid artery (solid line, artery present; dashed line, artery reduced or lost). The right side of each diagram illustrates the ectotympanic (stippled) and caudal entotympanic (open), which lie ventral to the structures on the left. Small arrows indicate direction of ontogenetic growth in felids, viverrids, and hyaenids. The morphotype is most closely approximated by the living aeluroid *Nandinia* of Africa. (After Hunt and Tedford 1993.)

Indies, and Madagascar, with *Genetta* alone surviving in southern Europe. They inhabit well-vegetated environments (forest, brushland, grassland), where they exploit arboreal, terrestrial, and aquatic habitats. Viverrines and hemigalines, although often good climbers, are predominantly terrestrial, whereas the paradoxures are arboreal. Arboreal species are commonly planigrade; terrestrial types tend to digitigrade. In their lack of cursorial specializations, which is reflected in a generalized postcranial anatomy, small body size, and (in many) unspecialized dentition, the viverrids have been regarded as skeletally primitive representatives of early Tertiary carnivorans.

In contrast to their present diversity, the Cenozoic fossil record of viverrids is poor. Moreover, because of the often fragmentary state of these fossils, the affinities of many taxa are problematical, and their biogeography remains less clear relative to other carnivoran families (Figure 15.11).

True fossil viverrids can be identified from basicranial and dental features. No living or fossil viverrid has more than two upper or lower molars, and premolars are not reduced in number; hence the dental formula is usually $I3/3$, $C1/1$, $P4/4$, $M2/2$. The upper molars generally lack strong internal cingula or hypocones, and often retain a developed parastyle. The lower carnassial usu-

ally maintains a primitive arrangement of the trigonid cusps: the paraconid-protoconid shearing blade is not developed to the extent seen in felids or most hyaenids. Similarly, the elongate upper carnassial and strong molar reduction of hyaenids and felids is absent. The basined heel of the lower carnassial usually displays a characteristic arrangement of three sharp cusps, including a hypoconulid, placed toward the rear of the talonid.

In living viverrids the ontogenetic growth pattern of the auditory bulla is diagnostic of the family (Figure 15.10). In early ontogeny, ectotympanic-rostral entotympanic contact produces the aeluroid thictic condition of the bulla (Hunt 1987). During ontogeny, the caudal entotympanic enlarges and grows forward over the conjoined ectotympanic-rostral entotympanic elements that form the anterior bulla chamber. The uniformity of this bulla pattern in living viverrids is particularly striking: it first appears in the early Miocene viverrid *Herpestides* from lacustrine deposits of the St.-Gerand sub-basin, France (Aquitanian, zone MN2a, 22–23 Ma), in which the bulla pattern and petrosal morph are fully modern in aspect (Hunt 1991). Notwithstanding the existence of a magnificent sample of early Miocene *Herpestides* crania, middle and late Miocene viverrids are rarely represented by skulls in Old World deposits. Before the Plio-Pleistocene, fossil viverrid skulls with well-preserved basicrania are poorly known, yet many lineages with fully modern basicrania must have been in existence, given the advanced state of the *Herpestides* auditory region in the early Miocene.

Fossil viverrids can be grouped into five temporal intervals:

1. 30(?) to 34 Ma, early Oligocene: protoviverrids (*Palaeoprionodon*) known from several skulls and a large number of mandibles from fissure fills at Quercy, France (see Hunt 1991:32), as well as from fragmentary dental material of *Palaeoprionodon* from Hsanda Gol, Mongolia.

2. 21 to 23 Ma, MN zone 2: a rich sample of crania, mandibles, and postcrania of *Herpestides*, from the Aquitanian of France, the oldest known viverrid with a modern auditory region.

3. 13 to 20 Ma, MN zones 3 to 8: the first diverse viverrids are identified from teeth in jaw fragments using dental traits common to living genera, and are accompanied by rare postcranial bones that suggest skeletons much like modern forms; no skulls with intact basicrania are known.

Viverra (subgenus *Viverrictis*), *Jourdanictis*, and *Semigenetta* are known from Europe; recently, *Semigenetta* has been found in China. In contrast to these rare (chiefly dental) remains is a completely articulated viverrid skeleton from freshwater limestone at Oeningen (MN8, ~13 Ma) in the British Museum, which represents the most complete European viverrid yet discovered; unfortunately, the skull is crushed and the basicranium is obscured. This large (15 kg) civetlike species demonstrates that by the middle Miocene some viverrids had attained a size equal to the larger living terrestrial civets (such as *Civettictis*).

The first African viverrids are known from this interval: these are repre-

sented primarily by dental remains from the early Miocene African rift sites of Rusinga and Songhor and nearby localities (Schmidt-Kittler 1987). Sites (such as Songhor) associated with the Tinderet volcanic complex (19.6 Ma) have yielded fossils attributed to *Stenoplesictis*, but these may be closer to the viverrid *Semigenetta*; sites (such as Rusinga) tied to the Rangwa volcano (17.8 Ma) have produced similar material but also dental remains referred to *Herpestides*, though the latter differ somewhat in details from the Aquitanian *Herpestides* of France. In the rift deposits these viverrids are associated with herpestids, and they indicate the oldest viverrid-herpestid differentiation known in the Old World, one that is based on dental evidence. When better fossils are found, the nature of the basicrania of these viverrids and herpestids will be of considerable interest.

4. 6 to 13 Ma, MN zones 9–13: although this is an interval with very few described viverrid remains, future discoveries in Asia may fill this gap. Few European and no African viverrids are certainly known. In Asia, Chinese faunas from Ertemte (MN13: Fahlbusch et al. 1983) and Lufeng (8 Ma, MN12) have produced good viverrid samples that are, however, yet to be described. In the Siwaliks, the “U-level” (~8 Ma) yielded a large viverrine and *Viverra chinjiensis*; the type of the latter, from the Chinji Siwaliks, probably came from the MN8–12 interval. In Europe a small viverrid attributed to *Semigenetta* (Petter 1976) is known at Can Llobateres (Vallesian, MN9).

5. 0 to 5 Ma, MN zones 14–17, MQ zones 1–2: Plio-Pleistocene discoveries of true viverrids in recent years, particularly in Africa, have greatly increased our knowledge of the family. Many of these species are large animals, equaling and even exceeding the living *Civettictis* (to 20 kg) and *Viverra* (to 12 kg) in body size (*Civettictis*, *Viverra*, and *Genetta* all appear for the first time in the African Pliocene). Most fossils not certainly attributable to these three genera belong to a complex of Eurasian and African species referred to “*Viverra*” (*leakeyi*, *peii*, *bakeri*, *chinjiensis*, *peprathi*), “*Vishnuictis*” (*durandi*, *salmon-tanus*), and “*Megaviverra*” (*carpathorum*, *apennina*). These fossils indicate that large viverrids existed in Europe as far north as central Czechoslovakia and in Asia to the latitude of Zhoukoudian, near Beijing. A number of these species belong to lineages in which large body size is coupled with a primitive shearing dentition and, in rare instances when the basicranium is present, a viverrid bulla. During this time interval and from this group evolve the largest viverrids that ever lived: the African endemic *Pseudocivetta* (whose skull is undescribed) and the south Asian *Vishnuictis durandi* (known from two crania), the former a dental omnivore with specialized crushing teeth, the latter a huge predatory wolflike viverrid with shearing teeth and an auditory bulla unquestionably of the viverrid type. *Vishnuictis durandi*, from the Siwaliks, also seems to occur in north China, where it has been called “*Viverra*” *peii*. Its skull form closely parallels the living *Civettictis*, which may be a close relative.

Recently, a skull and a large number of mandibles of a large predatory viverrid have been found at Langebaanweg, in South Africa (Hendey 1974):

the teeth correspond to those of the East African *Viverra leakeyi*, and the skull form of the Langebaanweg carnivoran is indeed similar to that of living *Viverra*. The Langebaanweg skull, when compared to a nearly complete Siwalik skull of *Vishnuictis durandi*, demonstrates that at least two large hypercarnivorous viverrids of very different skull form existed in the Plio-Pleistocene (Hunt, in press, b): (1) *durandi*, with a *Civettictis*-like cranium, a short snout, and an inflated frontal region; and (2) *leakeyi*, with a *Viverra*-like cranium, a long snout, and a normal frontal region. The genus *Vishnuictis* can be used for the former, and *Viverra* for the latter. Because the specialized crushing teeth of the African *Pseudocivetta* establish this genus as a unique hypocarnivorous lineage, the Plio-Pleistocene of the Old World now documents three lineages of large viverrids (*Viverra*, *Vishnuictis*, and *Pseudocivetta*).

The origins and fossil record of many of the living viverrids, such as the linsangs, paradoxures, hemigalines, and Malagasy *Eupleres*, *Fossa*, and *Cryptoprocta*, are largely unknown: at best, only Holocene records exist.

The Malagasy viverrids provide an important corroboration of the usefulness of the auditory bulla and associated basicranium in determining carnivoran affinities. On Madagascar the resident carnivorans are believed by several workers to have radiated from a single stock that reached the island at some time in the middle to late Cenozoic. Seven genera comprising eight species occur today on the island. The basicrania of the seven genera can be grouped in two categories: a viverrid bulla morph and a herpestid bulla morph. The genera *Fossa*, *Eupleres*, and *Cryptoprocta* have viverrid auditory regions, are larger animals ranging upwards from 1.5 to 12 kg, and are generally nocturnal to crepuscular in habit. In contrast, the genera *Galidia*, *Galidictis*, *Mungotictis*, and *Salanoia* have herpestid auditory regions, are smaller in size (usually <1.5–2 kg), and are chiefly diurnal (a species of *Galidictis*, however, is nocturnal). The larger animals are viverrids, the smaller ones herpestids. The island must have been invaded at least twice (by separate viverrid and herpestid stocks) at some time in the Cenozoic when the bulla morphs were already established. Because the viverrid morph had appeared by the early Miocene (Aquitanian, MN2a) in Europe, and on present evidence is unknown in the Oligocene, the colonization of Madagascar by viverrids would appear to be a post-Oligocene (probably early Neogene) event.

The first appearance of viverrids in Africa occurs in the early Miocene of Kenya and Saudi Arabia. But the time of migration of viverrids *sensu stricto* into Africa is less certain, for the reason that the diverse aeluroids found at Songhor, Rusinga, and other early Miocene sites (Schmidt-Kittler 1987) suggest some degree of *in situ* evolution, possibly a period of endemic development within the African continent. Demonstration of viverrid (or aeluroid) endemism in Africa or elsewhere must await a fuller knowledge of Oligocene faunas on that continent and in Eurasia. Consequently, the place of origin of viverrids in the Old World remains an open question.

Herpestidae

The living mongooses comprise about 17 genera of small (0.2–6 kg), chiefly terrestrial, digitigrade carnivorans, found mainly in Africa (*Herpestes* occurs in Africa, Asia Minor, southern Asia, and the East Indies). A Cenozoic radiation of mongooses in Africa is credited with the production of diverse species (Hendey 1974; Petter 1969) tending to predatory diurnal ground-dwellers, constituting at least seven gregarious genera (although some are nocturnal and solitary and can climb). Their fossil record is poor, with best representation in the Plio-Pleistocene of Africa, where about eight genera are known (Figure 15.11). As they have for viverrids, the sediments of the east African rift



Figure 15.11. Geographic distribution of late Eocene to Pleistocene fossil viverrids and herpestids. 1, Europe, Oligocene and Miocene viverrids and herpestids (*Palaeoprionodon*, *Herpestides*, *Semigenetta*, *Viverrictis*, *Jourdanictis*, *Leptoplesictis*). 2, Oligocene to Pliocene viverrids and herpestids: 2a, China and Mongolia (*Palaeoprionodon*, *Semigenetta*, *Viverra*, undescribed genera from Lufeng, south China); 2b, Bahe, north China (late Miocene herpestid); 2c, Europe, large late Pliocene viverrids (Czechoslovakia: Ivanovce, upper MN15; Italy: Villafranca d'Asti, lower MN16). 3, middle Miocene to Plio-Pleistocene viverrids and herpestids, Siwalik Group. 4, early Miocene to Plio-Pleistocene viverrids and herpestids, Kenya and Tanzania. 5, early Miocene viverrids, Israel and Saudi Arabia. 6, Pliocene viverrids and herpestids, Langebaanweg, south Africa (*Viverra*, *Genetta*, *Herpestes*). 7, early Miocene migration of viverrids and herpestids into Africa. 8, Neogene migration of separate viverrid and herpestid stocks to Madagascar. 9, middle Miocene viverrids, Turkey. 10, middle Miocene viverrid, north Africa (Beni Mellal, Morocco).

at Olduvai, Laetoli, and Omo have produced most of these carnivorans (*Helogale*, *Atilax*, *Ichneumia*, *Mungos*, and *Herpestes*), in association with early hominids and other mammals. South African Plio-Pleistocene sites have yielded *Herpestes*, *Cynictis*, *Crossarchus*, *Atilax*, and *Suricata*, only the first two of which extend into the Pliocene (Cooke 1964).

Early Miocene rift sediments in Kenya and Uganda, especially the Rusinga and Songhor localities, have produced the oldest African carnivoran assemblage, including six genera of small aeluroids. Schmidt-Kittler (1987) believes this is an immigrant assemblage, one that entered Africa during the later Oligocene or early Miocene. The oldest aeluroids, which occur at Songhor (~19.6 Ma), are already diverse; they include two hypercarnivores (*Miopronodon* and a ?stenoplesictine) and two hypocarnivores that may be early herpestids (*Legetetia*, *Kichechia*). Basicrania of all these genera, however, are unknown. Shortly thereafter, at the Rusinga sites (~17.8 Ma), a definite herpestid (*Leptoplesictis*) and a true viverrid (*Herpestides*) appear. This early Miocene diversity suggests a middle Cenozoic radiation of small aeluroids occurring earlier than previously believed. Because these small aeluroids occur in the faunas at Rusinga and Songhor with other definitive immigrants, such as amphicyonids and mustelids, they may well be immigrants themselves, but their diversity implies a degree of endemism or an arrival earlier than 19.6 Ma, in order to accommodate the differentiation of species observed at these sites.

Dental remains of *Leptoplesictis* in middle Miocene rocks (MN4) represent the oldest European herpestids. Because no complete skulls with basicrania have been found, the auditory region is unknown. These herpestids are small hypercarnivores, little different in tooth form and size from some of the living species of *Herpestes*. Both European and African *Leptoplesictis* are believed to be immigrants derived from southern Asia (Schmidt-Kittler 1987). Herpestids, however, are unknown before the late Miocene in Asia, where they occur in the Siwalik beds of Pakistan (*Herpestes*: Barry et al. 1980; Barry 1985) and in the Bahe fauna of north China (9–10 Ma, MN 10: Qiu 1989); these are the only Asian fossil herpestids, and they are as yet undescribed. Because postcranial remains of pre-Pliocene herpestids are extremely rare, almost nothing is known about their early skeletal structure.

The living herpestids share a number of derived anatomical traits, suggesting their origin from a common ancestral stock: (1) auditory bulla (Stage 3: Hunt 1987) with perbullar path of the internal carotid artery; (2) absence of marker chromosome; (3) specialized ear cartilages to close auditory meatus; (4) anal glands and pouches; and (5) a unique anastomosis of the internal carotid artery in the anterointernal corner of the auditory region (anastomosis Y of Bugge 1978). This complex of features, shared by all living mongooses, a morphologically uniform group, indicates that the African herpestid radiation stems from an ancestor possessing these traits, but as yet we have no fossil older than Pliocene displaying the single osteological feature (the auditory bulla) that might signal the presence of this character complex.

Hyaenidae

The four species of hyaenids living today are confined essentially to Africa, with only the striped hyena ranging to southern Asia. Striped and brown hyenas (*Hyaena*) weigh generally less than 60 kg, and the aardwolf (*Proteles cristatus*) less than 15 kg, but the spotted hyena (*Crocota crocuta*) may reach a weight of nearly 90 kg. Recent field studies (Kruuk 1972; Frank, this volume) have clarified the role of spotted hyenas as both active predators and scavengers, and it is clear from the diverse fossil record that the family has consistently included a wide range of feeding types.

Living hyaenids (*Hyaena*, *Crocota*) can be identified by their robust crushing premolars, elongate upper carnassial (with prominent parastyle), bladelike lower carnassial (metaconid lacking in *Crocota*, but present in *Hyaena*), and loss of M2/m2. M1/ is greatly reduced, serving only as a stop for the lower carnassial. These dental traits are obscured (if they ever existed) in the highly reduced dentition of the aardwolf, as a result of its myrmecophagy.

The hyaenid basicranium, particularly the distinctive auditory bulla, has remained anatomically conservative since the middle Miocene (Hunt and Solounias 1991). Although first believed to contain only a single chamber (Flower 1869), the unusual hyaenid bulla (Hunt 1974a, 1987; Hunt and Solounias 1991) was discovered by Pocock (1916) to be double-chambered. In *Crocota* and *Hyaena*, the bulla displays a unique ontogenetic growth pattern (Figure 15.10) in which the anterior (ectotympanic) chamber grows backward beneath a much smaller posterior chamber (*Proteles*, however, does not show the backward growth of the ectotympanic chamber, instead maintaining the anterior-posterior alignment of the chambers without any overgrowth of one chamber by the other). Almost all lineages of fossil hyaenids include at least one skull demonstrating the association of dentition with the unique hyaenid bulla pattern; hence the broad adaptive radiation of the family in the Miocene and Plio-Pleistocene is well documented by both basicranial and dental evidence.

An abundant fossil record of hyaenids stands in marked contrast to their present low diversity (Werdelin and Solounias 1991). Two major hyaenid assemblages can be recognized in time: (1) 5 to ~18 Ma, MN4b–13, early, middle, and late Miocene hyaenids (Figures 15.12, 15.13), a highly diverse radiation of Old World species (with good fossil samples in the Eurasian Vallesian-Turolian interval), which occupied bone-crushing, predatory, and generalized niches, paralleling in range of body size, dentition, and skull shape the New World canids of the same time interval; and (2) 0 to 5 Ma, MN14–17, MQ1–2, Plio-Pleistocene hyaenids (Figure 15.14), in essence, the living genera (extending back to about 3 Ma), which coexist with archaic bone-crushing (*Pachycrocota*) and hunting hyaenids (the *Euryboas-Chasmaporthetes* group). Basicranial structure is important to the demonstration of parallel hyaenid-canid radiations in the Old and New World.



Figure 15.12. Geographic distribution of early and middle Miocene fossil hyaenids. 1, Europe (*Protictitherium*, *Percrocuta*, *Miohyaena*). 2, Turkey and Georgia (*Protictitherium*, *Percrocuta*, *Miohyaena*). 3, Siwalik Group (*Percrocuta*). 4, northeast China (*Protictitherium*, *Percrocuta*, *Miohyaena*). 5, middle Miocene migration of hyaenids into Africa about 14 Ma (MN6/MN7 boundary): 5a, Saudi Arabia (*Percrocuta*); 5b, Ft. Ternan, Kenya (*Percrocuta*, *Protictitherium*); 5c, Morocco and Tunisia (*Protictitherium* and large hyaenid). The oldest African fossil hyaenids are from Ft. Ternan (Kenya), Al Jadidah (Saudi Arabia), and Beni Mellal (Morocco); these faunas correlate with the MN6/MN7 boundary or within European zone MN7.

Prior to 15 Ma, hyaenid fossils are rare, and the family appears to have been represented by two main branches (the diphyly of Chen and Schmidt-Kittler 1983, demonstrated on milk teeth): the *Percrocuta* species group and the central hyaenid stock (*Protictitherium*). The *Percrocuta* group is thought to have arisen from stenoplesictine aeluroids (Chen and Schmidt-Kittler 1983), whereas the origin of the protictitheres is uncertain. The structure and ontogenetic growth pattern of the auditory bulla (Figure 15.10) unites the *Percrocuta* group and the protictitheres in a monophyletic Hyaenidae (for a different view, see Werdelin and Solounias 1991).

Before ~18 Ma, no hyaenids can be identified in the fossil record. Hyaenids are found first in Europe, as rare dental remains from zones MN4b and MN5 in France (Ginsburg and Bulot 1982; Mein 1958; Stehlin 1925). Although not abundant, hyaenids occur in European Miocene to Pleistocene deposits: five different lineages are present in the Pleistocene (*Crocuta*, *Hyaena*, *Pachycrocuta* [two spp.], and the *Euryboas-Chasmaporthetes* group).

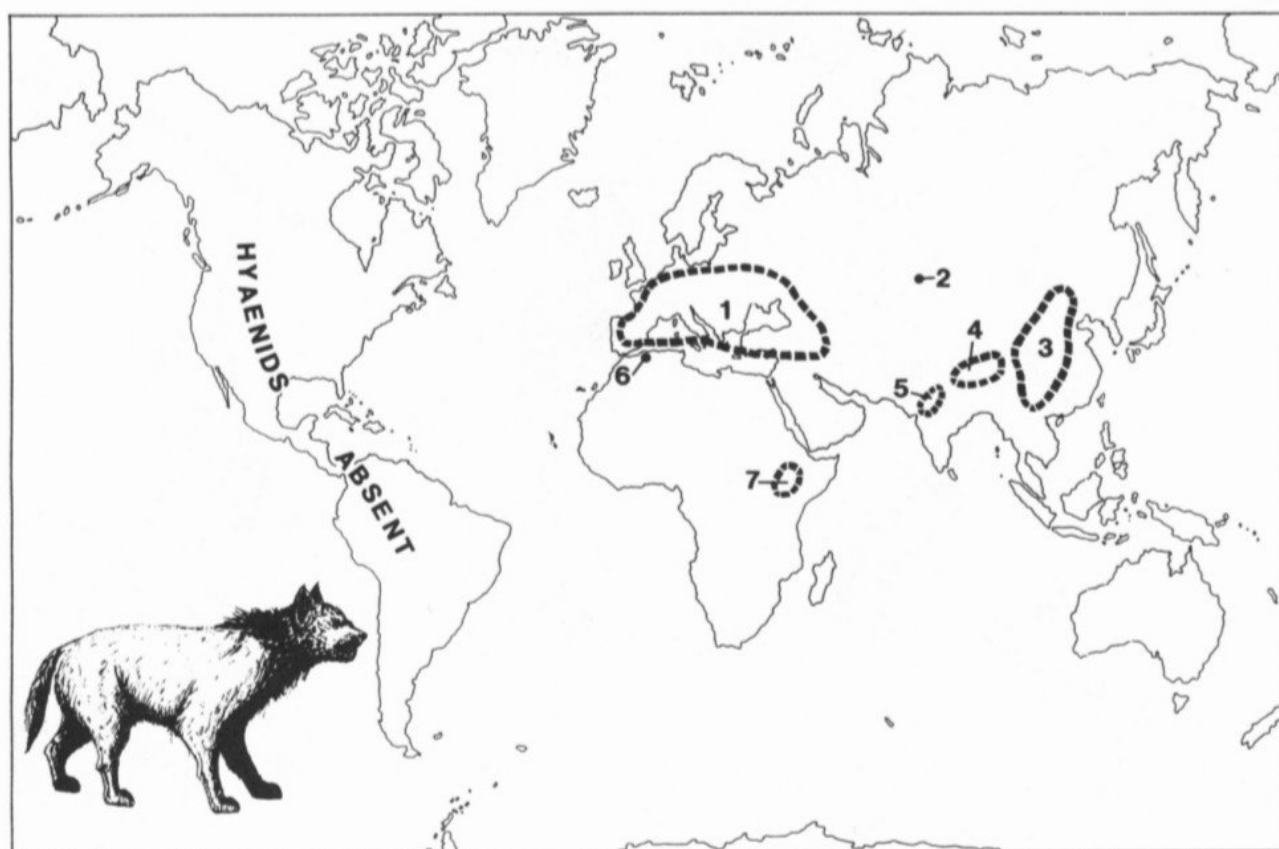


Figure 15.13. Geographic distribution of late Miocene fossil hyaenids. 1, Europe and southwest Asia (*Ictitherium*, *Thalassictis*, *Adcrocuta*, *Percrocuta*, *Miohyaena*, *Protictitherium*, *Plioviverrops*, *Lycyaena*). 2, central Asia (Pavlodar). 3, eastern China (*Ictitherium*, *Thalassictis*, *Adcrocuta*, *Palinhyaena*). 4, Tibet (Gyirong, Bulong). 5, Siwalik Group (*Percrocuta*, *Adcrocuta*, *Lycyaena*). 6, Algeria (Bou Hanifia). 7, Kenya (Lothagam, Baringo).

The first record of African hyaenids occurs at Fort Ternan in Kenya, where both *Protictitherium* and *Percrocuta* are dated at ~14 Ma (MN6/MN7 boundary: Schmidt-Kittler 1987). *Percrocuta* is also reported from the Al Jadidah fauna of Saudi Arabia, now placed at about the MN6/MN7 boundary (Savage 1989). Both *Percrocuta* and protictitheres occur from ~11–14 Ma in northern and eastern Africa at several sites (Beni Mellal, Beglia, Bou Hanifia, Fort Ternan, and Kabarsero). In Africa, diverse hyaenids appear for the first time at ~5 Ma, at or near the beginning of the Pliocene (Langebaanweg, Sahabi, Klein Zee, and Kanapoi).

The earliest record of an Asian hyaenid was believed to be a maxilla of *Protictitherium* from eastern China, probably MN4 or MN5 (Li et al. 1983), but Qiu (1989) reports that this record is in error and the maxilla should be referred to the viverrid *Semigenetta*. In Asia, the Turkish sites at Pasalar (early MN6) and Candir (late MN6) produced early records of both *Percrocuta* and protictitheres (14–15.5 Ma), and in north-central China the same two groups occur with *Miohyaena* in the Tongxin basin (MN6: Guan 1988; Harrison et al. 1991). In the Siwaliks, rare hyaenids from the Chinji levels could be as old

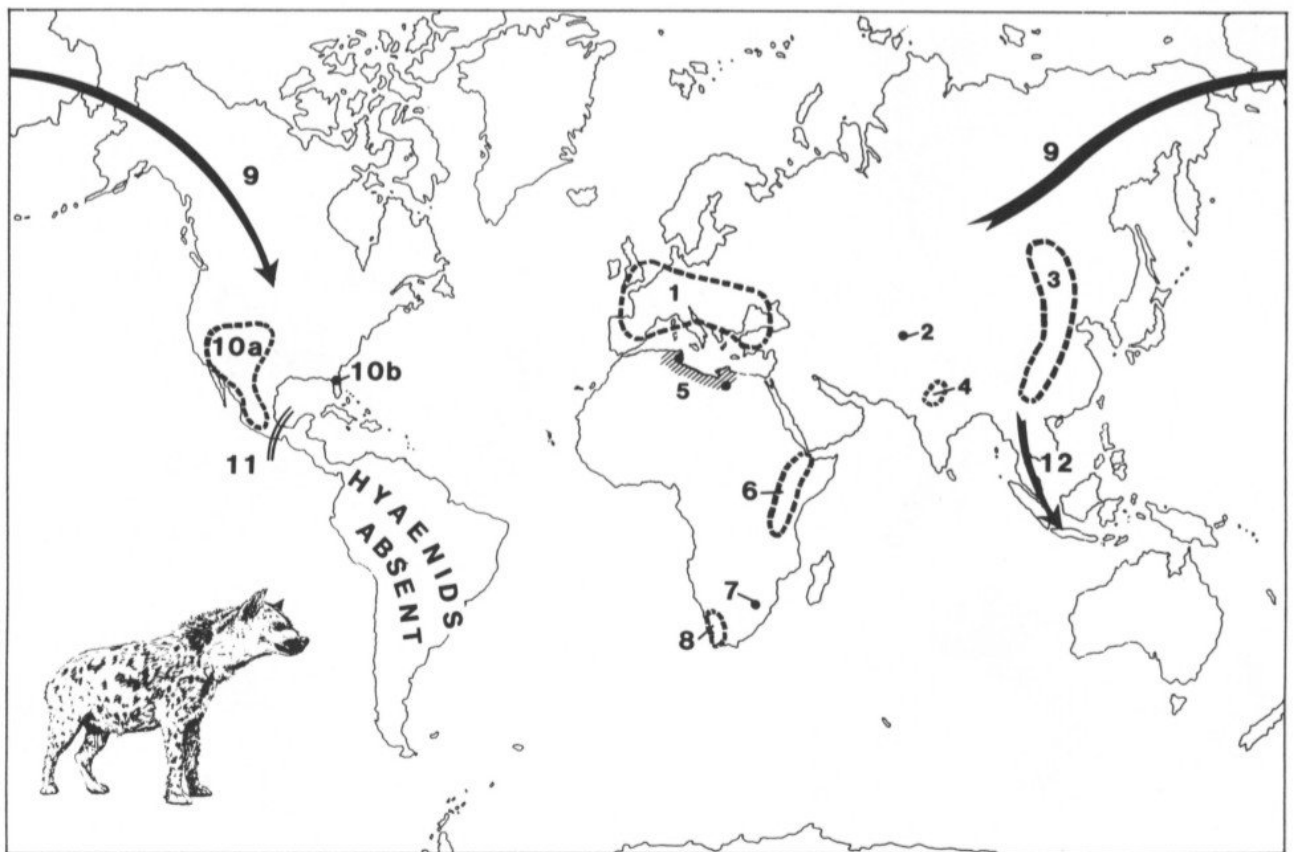


Figure 15.14. Geographic distribution of Pliocene fossil hyaenids. 1, Europe and southwest Asia (*Chasmaporthetes*, *Pachycrocuta*). 2, Tajikistan (Kuruksay). 3, eastern Asia (China and Baikal: *Chasmaporthetes*, *Pachycrocuta*). 4, Siwalik Group. 5, north Africa (Ain Brimba, Sahabi: *Chasmaporthetes*, *Pachycrocuta*). 6, Ethiopia, Kenya, Tanzania (*Pachycrocuta*, *Crocutea*, *Hyaena*). 7, south Africa (Sterkfontein 4, Makapansgat 3: *Chasmaporthetes*, *Pachycrocuta*, *Crocutea*, *Hyaena*). 8, south Africa (Kleinsee, Langebaanweg: *Hyaena*, *Chasmaporthetes*, "*Hyaena*" *namaquense*). 9, Pliocene migration of *Chasmaporthetes* to North America about 3.5 Ma. 10, North America (*Chasmaporthetes*): 10a, southwestern United States and Mexico (middle and late Pliocene, early Pleistocene); 10b, Florida (late Pliocene, early Pleistocene). 11, southern limit of fossil hyaenids in the New World. 12, Pleistocene migration of hyaenids (*Pachycrocuta*) to Java (Djetis, Sangiran).

as 13–14 Ma (13.2 Ma, the oldest Siwalik hyaenids: Barry and Flynn 1989). Just one basicranium is associated with any of these early occurrences: the holotype of *Percrocuta primordialis*, a skull with hyaenid auditory structure from Yinziling in the Tongxin basin (MN6: Qiu et al. 1988b). This specimen has recently been placed in a new genus, *Tongxinictis*, by Werdelin and Solounias (1991).

Collectively, these records demonstrate that the early hyaenids were small carnivorans widely distributed in Eurasia and Africa by 14–15 Ma, in the middle Miocene (MN6).

Three genera of hyaenids are at present recognized in Eurasia in the MN4–MN8 interval: *Protictitherium*, *Percrocuta*, and *Miohyaena*. The dentition of *Protictitherium* is the least specialized of these middle Miocene hyaenids: most fossils of the genus are distributed from western Europe to Asia Minor. In

contrast, the teeth of *Percrocuta* and *Miohyaena*, with their enlarged premolars and reduced molars, are already specialized for durophagous feeding. By MN6 these two genera exist across Eurasia. By the later middle Miocene (MN8), Eurasian hyaenids were remarkably diverse, as evidenced by the association of small, foxlike *Tungurictis* and large, bone-crushing *Percrocuta* species in the Tung Gur Formation of Inner Mongolia and in deposits of equivalent age elsewhere in Eurasia.

Diversity of body size was much greater in extinct hyaenids than it is in the living species. *Plioviverrops* from Samos and Pikermi was the size of a small fox, weighing ~2 kg; giant predaceous hyaenids (to 150 kg) evolved in the Plio-Pleistocene (*Pachycrocuta brevirostris*) and late Miocene of Eurasia (*Dinocrocuta gigantea*), the latter known to have had an upper carnassial length of over 5 cm and a basal skull length of 32 cm (Qiu, Xie, and Yan 1988a)! Dental diversity paralleled this range in body size. In early hyaenids, the two upper and two lower molars are present, the carnassials are not as exaggerated in either length or shearing structure, and the premolars are less robust, less inflated. From such a generalized dental pattern, bone-crushing hyaenids repeatedly evolve in the middle to late Cenozoic (*Percrocuta*, *Adcrocuta*, *Pachycrocuta*, *Dinocrocuta*, *Crocuta*), distinguished by the same suite of dental traits: robust crushing premolars, enormously elongated carnassials specialized for shear, and reduction of the rear molars (M2/m2 lost). As seen in living *Crocuta*, the bone-crushers represent the repeated evolution of an opportunistic feeding strategy: actively hunting prey and/or scavenging carcasses, breaking bones with their greatly enlarged premolars to exploit a nutrient source largely denied to other carnivorans. The evolution of similar canid ecomorphs (*Enhydrocyon*, *Osteoborus*, *Borophagus*, *Epicyon*) in North America lends support to this view. Alongside the bone-crushing hyaenids were generalized (*Ictitherium*, *Thalassictis*) and more predatory species (the *Euryboas-Chasmaporthetes* group), all of them today extinct and none represented by ecological equivalents among living hyaenids.

The hunting hyenas (*Chasmaporthetes*) are the only hyaenids to invade the New World, reaching North America (Fox Canyon, Kansas) ~3.5 Ma. These are Asian immigrants—the genus is known in China in the late Pliocene and early Pleistocene (Galiano and Frailey 1977), and an ancestral species occurs in the early Pliocene of Moldavia. No hyaenids have ever reached South America, notwithstanding the southernmost records of *Chasmaporthetes* in Mexico (Berta 1981).

Although hyaenid postcranials are not plentiful, they are much better represented than are those of viverrids and herpestids, and demonstrate that many lineages exhibit normally proportioned limbs (Gaudry 1862–63; Hunt and Solounias 1991); many species did not evolve the robust, exaggerated forequarters and low hindquarters that distinguish living *Crocuta* and *Hyaena*. The suggested ancestors of the striped hyena (*Hyaena hyaena*), found at Makapansgat (3 Ma) and Langebaanweg (5 Ma) in South Africa, retain normal limb proportions (Hendey 1974).

Postcranial skeletons of four genera (*Protictitherium*, *Ictitherium*, *Adcrocuta*, and *Plioviverrops*) of middle and late Miocene hyaenids demonstrate that digitigrady and a cursorial gait were common attributes of Miocene hyaenids, and that a digitigrade stance must have been achieved early in the history of the family (Hunt and Solounias 1991).

Felidae-Nimravidae

Felids are commonly considered the true cats of the Cenozoic, whereas nimravids are seen as catlike ecomorphs that parallel the felids in dental and cranial/postcranial osteology to a striking degree. The nimravids, however, can be shown from basicranial structure to be only distantly related to the felids (Neff 1983; Hunt 1987).

All fossil and living felids are short-faced predators with prominent biting canines and a tendency toward reduction and loss of teeth in front of and behind the carnassial pair, often with modification of the carnassials into simple shearing blades. It is this dental/cranial morph that is usually central to the popular concept of a "cat." In the postcranial skeleton, retractile claws accompany digitigrade feet, and the forelimbs retain a strong ability for pronation-supination as an aid in grasping prey. The felid basicranial and bulla structure is highly diagnostic in having a double-chambered aeluroid bulla with *septum bullae*, strong ontogenetic overgrowth of the anterior chamber of the bulla by the posterior (caudal entotympanic) chamber (Figure 15.10), and the bradynothictic pattern of ectotympanic-rostral entotympanic development during bulla ontogeny (Hunt 1987). Felids strongly reduce the internal carotid and basilar arterial blood supply to the brain, and utilize instead the external carotid route, commonly developing arterial retia along the orbital course of this artery to cool blood flowing to the brain.

In a superb survey of the living large felids, Neff summarizes the evolution of felid and nimravid carnivorans, setting her account against the artwork of Guy Coheleach (Neff and Coheleach 1982). Among the placental carnivorans, the nimravids and felids represent two entirely independent yet parallel Cenozoic radiations of catlike mammals (Figures 15.15–17). Nimravids, confined to the late Eocene to late Miocene, precede the felids in the development of their radiation, whereas felids diversify in the late Miocene to Pleistocene, an event that continues to be reflected today in their broad geographic distribution and rich species diversity. At first appearance, the nimravids are Holarctic in distribution; the earliest felids are confined to Eurasia.

Catlike parallels among the mammals evolve independently a number of times among both the placental (creodonts, carnivorans) and the marsupial (borhyaenids) carnivores. The earliest catlike mammals are Eocene hyaenodont creodonts (*Apataelurus*: Scott 1938; *Machaeroides*: Matthew 1909; Dawson et al. 1986) from western North America. Although known primarily

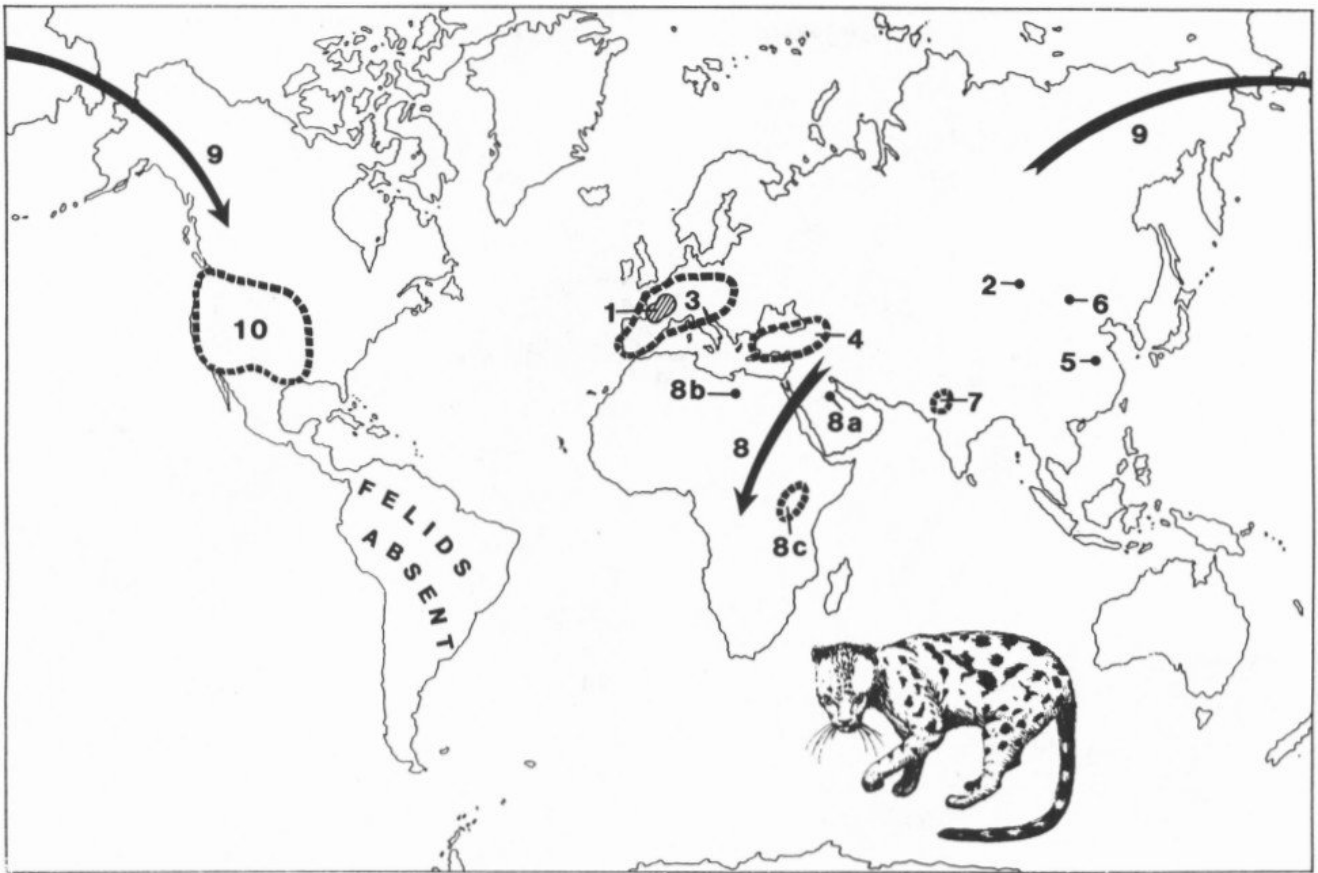


Figure 15.15. Geographic distribution of late Eocene to middle Miocene felids. 1, late Eocene to early Miocene, France (*Haplogale*, *Proailurus*). 2, early Oligocene, Hsanda Gol, Mongolia (proailurine). 3, early and middle Miocene, Europe (*Pseudaelurus*). 4, middle Miocene, Turkey and Georgia (Belometcheskaya, *Pseudaelurus*). 5, early Miocene, China (Xiacaowan, *Pseudaelurus*). 6, middle Miocene, Inner Mongolia (Tung Gur, *Metailurus*, ?machairodont). 7, middle Miocene, Siwalik Group (*Sivasmilus*, *Sivaelurus*, *Vishnufelis*, "Vinayakia"). 8, early Miocene migration of felids into Africa about 19.6 Ma: 8a, early Miocene, Saudi Arabia (*Pseudaelurus*); 8b, early Miocene, Libya (felid); 8c, early Miocene, Kenya (*Afrosmilus*). 9, Miocene migration of felids to North America about 16–17 Ma. 10, middle Miocene, western North America (*Pseudaelurus*).

from only a few jaws, the group is best represented by a skull, mandibles, and associated postcrania from the Bridger Eocene of Wyoming (Gazin 1946).

These creodonts are succeeded in time by the Oligocene and Miocene radiation of nimravid cats of the northern continents (Cope 1880; Neff 1983). Skeletons of nimravids, many essentially complete, are often found preserved in the White River Group of the North American midcontinent and in the John Day beds of Oregon. Nimravids are largely extinct by the end of the early Miocene, but a single subfamily, the Barbouriinae, persists in Eurasia (*Sansanosmilus*) and North America (*Barbouriina*) until the late Miocene. Only a single nimravid (*Syrtosmilus*) reached Africa (Ginsburg 1978), the only record of the family on the southern continents. *Syrtosmilus* occurs in the Gebel Zelten fauna, Libya, in the late early Miocene, MN3b or MN4a (Savage 1989). There is no evidence that nimravids penetrated farther south into cen-

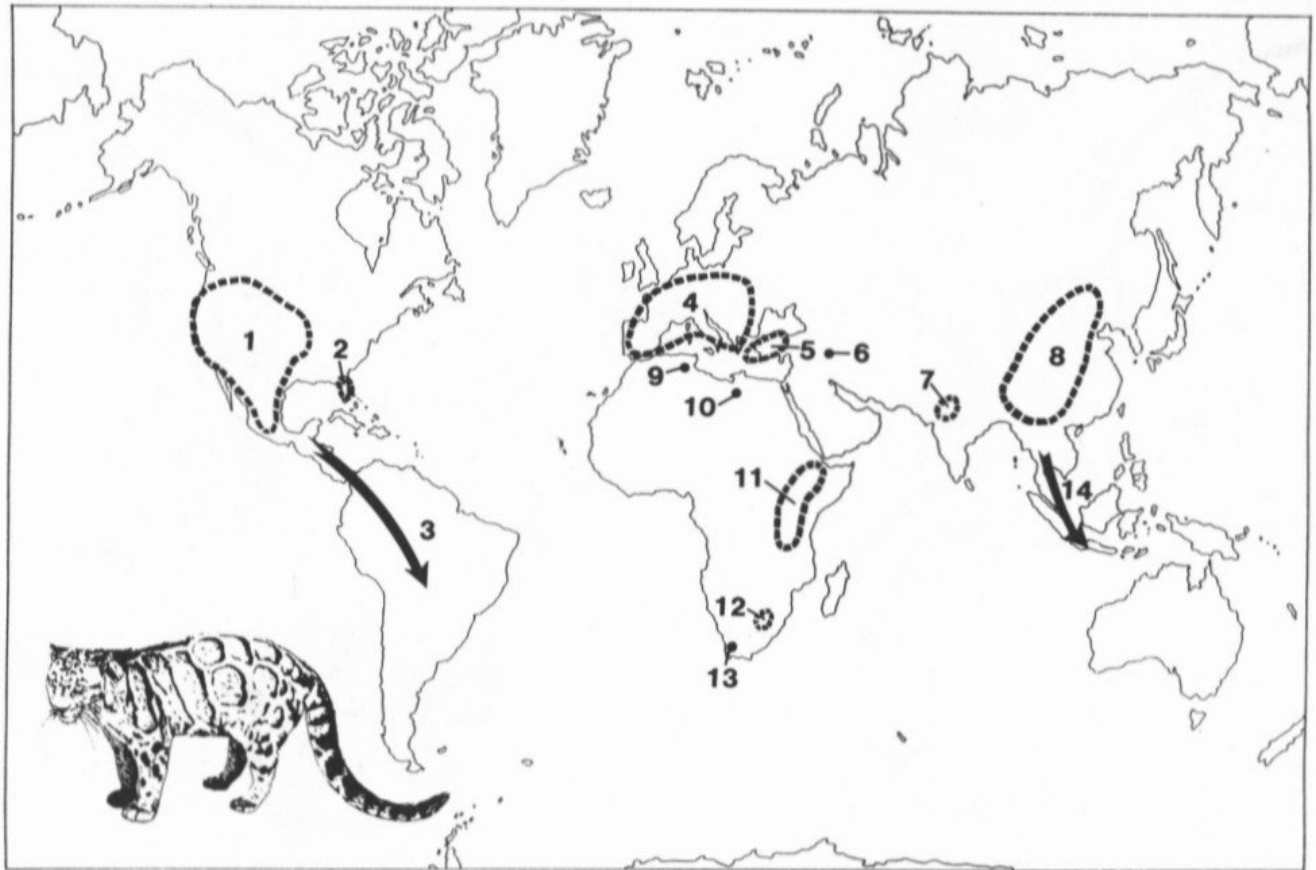


Figure 15.16. Geographic distribution of late Miocene and Pliocene felids. 1, western North America (*Homotherium*, *Machairodus*, *Megantereon*, *Nimravides*, *Dinofelis*, *Panthera*, *Felis*, *Lynx*, "Acinonyx"). 2, Florida (*Homotherium*, *Machairodus*, *Megantereon*, *Nimravides*, *Smilodon*, *Lynx*). 3, late Pliocene migration of felids to South America about 1.9–2.0 Ma (*Felis*, *Smilodon*). 4, Europe (*Homotherium*, *Machairodus*, *Megantereon*, *Dinofelis*, *Panthera*, *Felis*, *Lynx*, *Acinonyx*, *Metailurus*, *Pontosmilus* (= *Paramachairodus*). 5, Turkey (*Megantereon*, *Machairodus*, *Miomachairodus*, *Metailurus*, *Felis*). 6, Iran (Maragheh: *Machairodus*, *Pontosmilus*, *Metailurus*, *Felis*). 7, Siwalik Group (*Machairodus*, *Megantereon*, ?*Homotherium*, *Panthera*, *Felis*, "Propontosmilus," "Sivafelis," "Aeluropsis"). 8, eastern China and Tibet (*Homotherium*, *Machairodus*, *Miomachairodus*, *Megantereon*, *Dinofelis*, *Felis*, *Lynx*, *Acinonyx*, *Metailurus*, *Pontosmilus*). 9, Tunisia (*Machairodus*). 10, Libya (*Machairodus*). 11, East Africa (*Homotherium*, *Machairodus*, *Megantereon*, *Dinofelis*, *Panthera*, *Felis*, *Acinonyx*). 12, south Africa (Sterkfontein 4 and Makapansgat 3: *Homotherium*, *Megantereon*, *Dinofelis*, *Panthera*, *Felis*, *Acinonyx*). 13, south Africa (Langebaanweg: *Homotherium*, *Machairodus*, *Dinofelis*, *Felis*). 14, Pleistocene migration of *Homotherium* and *Megantereon* to Java.

tral or southern Africa, and nimravids are extinct worldwide by the beginning of the Pliocene.

Although the earliest true felids (*Proailurus*, *Haplogale*: Ginsburg 1983) exist in Europe and Asia alongside the nimravids during the Oligocene and early Miocene, they are not diverse, and it is not until the middle Miocene decline in nimravid diversity that felids begin their radiation, culminating in the great Plio-Pleistocene sabertooths (*Machairodus*, *Homotherium*, *Megantereon*, *Smilodon*) and other true cats with normal canines (*Felis*, *Panthera*, *Metailurus*, *Acinonyx*).



Figure 15.17. Geographic distribution of late Eocene to late Miocene fossil nimravids. 1, western North America, late Eocene to late Miocene (*Dinictis*, *Hoplophoneus*, *Nimravus*, *Eusmilus*, *Dinaelurus*, *Barbourofelis*). 2, Florida, late Miocene (*Barbourofelis*). 3, Europe, late Eocene to late Miocene (late Eocene to Oligocene: *Nimravus*, *Eusmilus*, *Dinailurictis*, *Quercylurus*, *Eofelis*; Miocene, 10.6–18 Ma: *Prosansanosmilus*, *Sansanosmilus*). 4, southwest Asia, Oligocene nimravids (Benara, Aral Sea, Askazansor). 5, Mongolia, Oligocene (Hsanda Gol, Khoer-dzan: *Nimravus*). 6, north China, middle Miocene (*Sansanosmilus*). 7, south China, ?Eocene (Bose Basin). 8, Siwalik Group, middle to late Miocene (7.4 to >15.1 Ma). 9, early Miocene migration of nimravids to north Africa (Libya: *Syrtosmilus*).

True felids are not found in the Oligocene of North America, but first appear in the Oligocene of Europe (Quercy) and Asia (Hsanda Gol). These earliest felids, the proailurines, are small, none larger than a lynx. They spread to North America ~16–17 Ma, in the late early Miocene or early middle Miocene, when a proailurine first appears at Ginn Quarry in western Nebraska. This is the earliest record of a New World felid (Hunt 1987). In the middle Miocene of North America, the descendants of the proailurines, the pseudaelurine felids (*Pseudaelurus*), do not exceed the size of living lynx and leopards and are not diverse. By the late Miocene, North American and Eurasian felids display a wider range in size and diversity, heralding the Plio-Pleistocene radiation of the family. Felids of large size do not appear and diversify until the extinction of the great amphicyonids and hemicyonine ursids that dominate the middle Miocene and early late Miocene faunas of Holarctica.

True felids migrate to Africa in the early Miocene. Sediments of the East

African rift system yield the oldest African felids (*Afrosmilus*), at Songhor (MN3, ~19.6 Ma) and Rusinga (MN4, ~17.8 Ma in Schmidt-Kittler 1987; 17.5–18.0 Ma in Savage 1989; Drake et al. 1988). Because of its incipient sabertooth features, *Afrosmilus* differs sufficiently from the typical Holarctic Miocene felid *Pseudaelurus* to suggest a separate lineage. A species of *Pseudaelurus* is also recorded in the Dam Formation of Saudi Arabia, at the As-Sarrar locality (Thomas et al. 1982; Savage 1989) at about MN4a. These two felid genera at MN4 sites in Africa and Saudi Arabia indicate that at least two lineages are present at the earliest appearance of the family on that continent in the early Miocene.

The earliest record of felids in South America occurs in the Vorohue Formation of Argentina, where fossils of two genera (*Felis vorohuensis*, *Smilodon*) appear as part of a dispersal event in the late Pliocene, ~1.9–2.4 Ma (Marshall 1985; Marshall et al. 1984; Marshall and Sempere 1993). *Felis vorohuensis*, a small cat represented by upper and lower jaw fragments and a partial postcranial skeleton, is regarded as the oldest certainly determined felid in South America (Berta 1983). This fossil species seems to be much like the living small Pampas cat, *Felis colocolo*. The reported occurrence of *Smilodon* in the Vorohue Formation is disputed (Berta 1985:2); the material in question seems to have come from younger Ensenadan-age sediments.

By the Ensenadan mammal age, the puma (*Felis concolor*), jaguar (*F. onca*), and sabercat (*Smilodon*) are all present in South America (Marshall et al. 1984:20). Among these large cats, only *Smilodon* becomes extinct prior to the Holocene. The extinction of the marsupial borhyaenid carnivores by the end of the Chapadmalalan age, succeeded in the immediately overlying deposits by the arrival of true felids, is considered evidence of ecologic replacement of marsupial by placental carnivores (Marshall 1978a; Berta 1988). The absence of felids in South America for most of the Cenozoic led to the evolution among the carnivorous borhyaenids of a marsupial sabertooth cat, *Thylacosmilus* (Huayquerian and Montehermosan mammal ages), closely paralleling in cranial anatomy the sabertooths of the northern continents (Riggs 1934; Marshall 1976; Turnbull and Segall 1984).

The evolutionary radiation of felids has taken place primarily over the last 10 million years. During that interval (late Miocene to Recent), felid cats with saber canines evolved, paralleling the earlier nimravid sabertooth cats and sabertooth marsupials. Sabertooth cats, whether marsupial or placental, share in a number of osteological traits that suggest the different lineages are ecomorphs: all possess elongate, bladelike canines, shearing cheek teeth, short cranium with developed mastoid and occipital regions, massive neck and forequarters, and powerful forelimbs with good ability for rotation (supination-pronation) of the lower forelimb. Convergence in these skeletal traits indicates a common sabertooth feeding behavior, one in which the sabers are driven into the prey using particularly strong head and neck musculature, and in which prey capture and manipulation are accomplished through powerful forelimbs

and clawed feet. Postcranial skeletons demonstrate that no sabertooth is a cursor; hence these animals must have attacked quickly from cover, and could run for only short distances. Sabertooths persisted nearly to the present: *Homotherium* is known from the late Pleistocene Friesenhahn Cave in Texas (Rawn 1981; Meade 1961), and *Smilodon* was probably living into the early Holocene (Kurtén and Anderson 1980).

Summary

Once the major lineages of the Carnivora are identified and traced through Cenozoic time, a clearer picture of the geographic distribution and evolution of carnivorous mammals emerges. Important to this new biogeography is the sharper definition of the doglike arctoid and cynoid carnivorans: the canids, amphicyonids, and ursids. In earlier mammalian classifications, particularly that of G. G. Simpson in 1945, these lineages were seriously confused, resulting in the mistaken impression that "canids," a waste-basket taxon for the doglike Carnivora, were broadly distributed on the northern continents. Endemism went largely unrecognized and was restricted to the level of genera and species. Through the efforts of French and American paleontologists in the 1960s, the defining features of true canids (primarily basicranial) were recognized for the first time, and it then became apparent that the family had been geographically restricted to the New World until the late Miocene, immigrating to Eurasia only about 9 million years ago. The numerous species of doglike carnivorans of the Old World were in fact not canids, but amphicyonids and ursids. The ursids and amphicyonids, together with the durophagous and carnivorous hyaenids, filled the niches in the Old World so thoroughly exploited by canids in the Americas. Indeed, the endemism of doglike carnivorans at the level of the family was a key aspect of Holarctic carnivoran biogeography unappreciated by Simpson and his contemporaries.

Similarly, the study of basicranial structure has resolved and better defined the limits of the aeluroid families, thus contributing to clarification of aeluroid biogeography. In contrast to arctoids, the aeluroids remain largely confined to the Old World throughout the Cenozoic. Only felids successfully colonize the New World, entering North America ~16–17 Ma and migrating to South America within the last 2 million years. Despite their marked diversity and broad distribution in the Old World, only a single hyaenid species penetrated the Americas, and is limited to the southern United States and northern Mexico during the Pliocene and early Pleistocene. The small aeluroids, the herpestids and viverrids, are confined to Eurasia and Africa throughout their history and failed to invade the New World.

The dominance of placental creodonts and absence of carnivorans in the Oligocene of Africa, and the sudden appearance there of Carnivora of several families (both arctoids and aeluroids) in the early Miocene, suggest to most

biogeographers that the Carnivora entered Africa as migrants in the earliest Miocene, during the initiation of major faunal exchange between Eurasia and Africa. By the end of the Miocene, creodonts were extinct in Africa. The placental carnivorans radiated rapidly during the Miocene, becoming dominant and widely distributed in the Plio-Pleistocene. The modern African carnivoran fauna is a relict of this late Cenozoic radiation.

In South America during the Cenozoic, the borhyaenid marsupials and phororhacoid birds occupied the principal niches for carnivores, becoming extinct during the 2.0–2.5 Ma interval. Placental carnivores of the arctoid, cynoid, and aeluroid groups entered South America from the north during the great Plio-Pleistocene faunal interchange. Rare arctoids of the *Cyonasua* group reach South America ~7 Ma, followed by invading mustelids, procyonids, canids, felids, and ursids at ~2–2.5 Ma. Hence the modern carnivore fauna of South America is, as in Africa, the product of late Cenozoic tectonic and climatic events.

The Australasian region throughout Cenozoic time was the province of marsupial carnivores, and on present evidence never felt the impact of placental carnivorans until the advent of man.

Carnivoran biogeography reflects the isolation of the continents in the earlier Cenozoic, an isolation created not only by the spatial separation of the continental landmasses, but also by barriers to migration resulting from the invasion of the land by epeiric seas. As continental connections were established in the middle and late Cenozoic (and as epeiric seas withdrew), the migration of placental Carnivora into the southern continents apparently replaced the endemic creodonts of Africa and borhyaenids of South America. These placentals belonged to established and well-defined Holarctic groups: the arctoids, aeluroids, and cynoids.

Less well known is the succession of placental carnivoran faunas on the two northern continents: (1) late Eocene-Oligocene (~24–40 Ma): in Eurasia a hyaenodont-nimravid-arctoid fauna (with sparse aeluroids); in North America a hyaenodont-nimravid-canid fauna (with few arctoids); (2) early Miocene (~18–24 Ma): in Eurasia an arctoid (amphicyonids, small species of ursids, mustelids, and procyonids) and aeluroid (all four of the living families present for the first time) fauna; in North America an arctoid (chiefly an amphicyonid-mustelid assemblage with rare ursid and procyonid species) and canid fauna; (3) middle Miocene (~9–18 Ma): in Eurasia an arctoid (large forms are amphicyonids and hemicyonine ursids, small species include mustelids, procyonids, other ursids) and aeluroid fauna; in North America an arctoid (large amphicyonids and hemicyonines, smaller mustelids, procyonids, and rare ursine ursids) and canid fauna (with rare felids); and (4) late Miocene to Recent (~9 Ma to the present): in Eurasia, arctoids and aeluroids, with introduction of canids at 9 Ma; in North America, canids and arctoids (ursids, mustelids, and procyonids), with diverse Plio-Pleistocene felids and a single hyaenid. These faunas of Holarctic carnivorans opportunistically migrated to the south-

ern continents when dispersal was possible: in Africa these successive carnivoran faunas can be recognized in Miocene to Recent assemblages; in South America only the most recent fauna reached that continent because of the absence of an effective land connection prior to the middle Pliocene.

Our perceptions of paleobiogeographic patterns are strongly influenced by the known geographic distribution of fossils (Figures 15.3–9, 15.11–17). The rich carnivoran samples of the Holarctic continents have in recent years provided a reliable framework for new biogeographic inferences concerning middle to late Cenozoic carnivoran distributions. At the higher taxonomic levels these patterns are now confirmed on a global basis. New discoveries from Asia, however, are necessary to complete our knowledge of the Palearctic region, especially with regard to Asia's role as a place of origin for a number of supposedly immigrant groups appearing abruptly in Europe and North America during the late Paleogene and early Neogene.

Emerging evidence from Africa and South America has begun to clarify the timing of faunal transformations on the southern continents during the Cenozoic. In South America, future work can focus profitably on a more detailed resolution of the Plio-Pleistocene chronology of carnivoran immigration during the last 2.5 million years. In Africa, changes in the carnivore component of the faunas from the Paleogene into the Neogene are important and still obscure, and will only be comprehended through new discoveries in the field. The nature of African and Asian carnivore faunas and evolution is perhaps the principal challenge within our newly emergent concept of carnivoran paleobiogeography.

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References

- Archer, M. 1976. The basicranial region of marsupicarnivores (Marsupialia), interrelationships of carnivorous marsupials, and affinities of the insectivorous marsupial peramelids. *J. Linn. Soc. London (Zool.)* 59(3):217–322.
- Baker, M. A. 1979. A brain-cooling system in mammals. *Sci. Amer.* 240(5):130–139.
- Baker, M. A. 1980. Anatomical and physiological adaptations of panting mammals to heat and exercise. In: S. M. Horvath and M. K. Yousef, eds. *Environmental Physiology: Aging, Heat and Altitude*, pp. 121–146. New York: Elsevier North Holland.
- Baker, M. A. 1982. Brain cooling in endotherms in heat and exercise. *Ann. Rev. Physiol.* 44:85–96.
- Barnes, L. G., Domning, D. P., and Ray, C. E. 1985. Status of studies on fossil marine mammals. *Marine Mamm. Sci.* 1(1):15–53.
- Barry, J. C. 1985. Les variations des faunes du Miocène moyen et supérieur des formations des Siwaliks au Pakistan. *L'Anthropologie (Paris)* 89(3):268.
- Barry, J. C. 1987. Large carnivores (Canidae, Hyaenidae, Felidae) from Laetoli. In: M. D. Leakey and J. M. Harris, eds. *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 235–258. Oxford: Clarendon Press.
- Barry, J. C. 1988. *Dissopsalis*, a middle and late Miocene proviverrine creodont (Mammalia) from Pakistan and Kenya. *J. Vert. Paleontol.* 8(1):25–45.
- Barry, J. C., Behrensmeyer, A. K., and Monaghan, M. 1980. A geologic and biostratigraphic framework for Miocene sediments near Khaur village, northern Pakistan. *Yale Peabody Mus. Postilla* 183(1–2):1–19.
- Barry, J. C., and Flynn, L. J. 1989. Key biostratigraphic events in the Siwalik sequence. In: E. H. Lindsay, V. Fahlbusch, and P. Mein, eds. *European Neogene Mammal Chronology*, pp. 557–571. New York: Plenum Press.
- Barry, J. C., Lindsay, E. H., and Jacobs, L. L. 1982. A biostratigraphic zonation of the Middle and Upper Siwaliks of the Potwar Plateau of northern Pakistan. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 37:112.
- Baskin, J. 1982. Tertiary Procyoninae (Mammalia, Carnivora) of North America. *J. Vert. Paleontol.* 2(1):71–93.
- Baskin, J. 1989. Comments on New World Tertiary Procyonidae (Mammalia, Carnivora). *J. Vert. Paleontol.* 9(1):110–117.
- Beaumont, G. de. 1968. Note sur la région auditive de quelques carnivores. *Archiv. des Sci., Genève* 21(2):213–223.
- Beaumont, G. de. 1982. Brèves remarques sur la dentition de certains ursidés (mammifères). *Archiv. des Sci., Genève* 35(2):153–156.
- Beaumont, G. de. 1984. Des dents d'*Amphicyon* (mammifère, carnivore, Ursidé) du Turolien basal de Kohfidisch, Burgenland, Autriche. *Archiv. des Sci., Genève* 37(1):75–83.
- Berta, A. 1981. The Plio-Pleistocene hyaena *Chasmaporthetes ossifragus* from Florida. *J. Vert. Paleontol.* 1(3–4):341–356.
- Berta, A. 1983. A new species of small cat (Felidae), from the late Pliocene–early Pleistocene (Uquian) of Argentina. *J. Mammal.* 64(4):720–725.
- Berta, A. 1985. The status of *Smilodon* in North and South America. *Contrib. Sci., Nat. Hist. Mus., Los Angeles Co.* 370:1–15.
- Berta, A. 1988. Quaternary evolution and biogeography of the large South American Canidae (Mammalia: Carnivora). *Univ. California Publ. Geol. Sci.* 132:1–149.

- Bien, M., and Chia, L. 1938. Cave and rock-shelter deposits in Yunnan. *Bull. Geol. Soc. China* 18(4):325–347.
- Boaz, N., Gaziry, A., and El-Arnauti, A. 1979. New fossil finds from the Libyan Upper Neogene site of Sahabi. *Nature* 280:137–140.
- Bonis, L. de. 1981. Contribution à l'étude du genre *Palaeogale* Meyer (Mammalia, Carnivora). *Ann. Paléontol.* 67(1):37–56.
- Bonis, L. de, and Guinot, Y. 1987. Le gisement de vertébrés de Thézels (Lot) et la limite Oligo-Miocène dans les formations continentales du bassin d'Aquitaine. *München Geowiss. Abhandl.* 10:49–58.
- Bryant, H. N. 1993. Carnivora and Creodonta of the Calf Creek Local Fauna (late Eocene, Chadronian), Cypress Hills Formation, Saskatchewan. *J. Paleontol.* 67(6):1032–1046.
- Bugge, J. 1978. The cephalic arterial system in carnivores, with special reference to the systematic classification. *Acta Anat.* 101:45–61.
- Chen, G., and Schmidt-Kittler, N. 1983. The deciduous dentition of *Percrocuta* Kretzoi and the diphyletic origin of the hyaenas (Carnivora, Mammalia). *Paläont. Zeitschr.* 57:159–169.
- Cirot, E., and Bonis, L. de. 1992. Revision du genre *Amphicynodon*, carnivore de l'Oligocène. *Palaeontographica* (Abt. A) 220:103–130.
- Cirot, E., and Bonis, L. de. 1993. Le crâne d'*Amphictis ambiguus* (Carnivora, Mammalia): Son importance pour la compréhension de la phylogénie des mustéloïdes. *C. R. Acad. Sci. Paris* (ser. II) 316:1327–1333.
- Clark, J., and Guensburg, T. 1972. Arctoid genetic characters as related to the genus *Parictis*. *Fieldiana: Geol.* 26(1):1–71.
- Cooke, H. B. S. 1964. The Pleistocene environment in southern Africa. In: D. H. S. Davis, ed. *Ecological Studies in Southern Africa*, pp. 1–23. The Hague: Junk.
- Cope, E. D. 1880. On the extinct cats of America. *Amer. Nat.* 14(12):833–858.
- Corvinus, G., and Hendey, Q. B. 1978. A new Miocene vertebrate locality at Arrisdrift in South West Africa (Namibia). *Neue Jahrb. Geol. Paläont. Monatshefte*, Heft 4:193–205.
- Crusafont-Pairo, M. 1950. El primer representante del genero "Canis" en el pontiense Eurasiatico ("Canis" *cipio* nova sp.). *Bolet. Real Soc. Espan. Hist. Natur.* 48(1):43–51.
- Davis, D. D. 1964. The Giant Panda: A morphological study of evolutionary mechanisms. *Fieldiana: Zool., Mem.* 3:1–339.
- Davis, D. D., and Story, H. E. 1943. The carotid circulation in the domestic cat. *Zool. Ser., Field Mus. Nat. Hist.* 28:1–47.
- Dawson, M. R., Stucky, R. K., and Krishtalka, L. 1986. *Machaeroides simpsoni*, new species, oldest known sabertooth creodont (Mammalia), of the Lost Cabin Eocene. *Contrib. Geol., Univ. Wyoming*, Spec. Paper 3:177–182.
- Dehm, R. 1950. Die Raubtiere aus dem Mittel-Miocän (Burdigalium) von Wintershof-West bei Eichstätt in Bayern. *Abhandl. Bayerisch. Akad. d. Wiss. (Math.-naturwiss. Klasse)*, N.F., Heft 58:1–141.
- Denison, R. H. 1938. The broad-skulled Pseudocreodi. *Ann. New York Acad. Sci.* 37:163–257.
- Drake, R., Van Couvering, J., Pickford, M., Curtis, G., and Harris, J. 1988. New chronology for the Early Miocene mammalian faunas of Kisingiri, Western Kenya. *J. Geol. Soc. London* 145:479–491.
- Emry, R. J. 1992. Mammalian range zones in the Chadronian White River Formation at Flagstaff Rim, Wyoming. In: D. Prothero and W. A. Berggren, eds. *Eocene-Oligocene Climatic and Biotic Evolution*, pp. 106–115. Princeton, N.J.: Princeton Univ. Press.

- Fahlbusch, V., Qiu Z., and Storch, G. 1983. Neogene mammalian faunas of Ertemte and Harr Obo in Nei Mongol, China. *Scientia Sinica* (Ser. B) 26(2):205–224.
- Fay, F. H., Rausch, V. R., and Feltz, E. T. 1967. Cytogenetic comparison of some pinnipeds (Mammalia: Eutheria). *Canadian J. Zool.* 45:773–778.
- Fejfar, O. 1989. The Neogene VP sites of Czechoslovakia. In: E. H. Lindsay, V. Fahlbusch, and P. Mein, eds. *European Neogene Mammal Chronology*, pp. 211–236. New York: Plenum Press.
- Flower, W. H. 1869. On the value of the characters of the base of the cranium in the classification of the order Carnivora. *Proc. Zool. Soc. London* 1869:4–37.
- Frackowiak, H. 1989. Das Rete mirabile der Arteria maxillaris des Löwen (*Panthera leo* L. 1758). *Anat. Histol. Embryol.* 18:342–348.
- Galiano, H., and Frailey, D. 1977. *Chasmaporthetes kani*, new species from China, with remarks on phylogenetic relationships of genera within the Hyaenidae (Mammalia, Carnivora). *Amer. Mus. Novit.* 2632:1–16.
- Gaudry, A. 1862–63. *Animaux fossiles et géologie de l'Attique*. Carnivores, pp. 37–120. Paris.
- Gazin, C. L. 1946. *Machaeroides eothen* Matthew, the sabertooth creodont of the Bridger Eocene. *Proc. U.S. Natl. Mus.* 96:335–347.
- Gingerich, P., and Deutsch, H. 1989. Systematics and evolution of early Eocene Hyaenodontidae (Mammalia, Creodonta) in the Clark's Fork Basin, Wyoming. *Contrib. Mus. Paleontol., Univ. Michigan* 27(13):327–391.
- Gingerich, P., and Sahni, A. 1979. *Indraloris* and *Sivaladapis*: Miocene adapid primates from the Siwaliks of India and Pakistan. *Nature* 279(5712):415–416.
- Ginsburg, L. 1977. Les carnivores du Miocène de Beni Mellal (Maroc). *Géol. Mediterr.* 4(3):225–240.
- Ginsburg, L. 1978. *Syrtsmilus syrtensis*, n. gen., n. sp., Félidé machairodontiforme du Burdigalien de Libye. *C. R. somm. Soc. Géol. France*, 1978, 2:73–74.
- Ginsburg, L. 1980. *Hyainailouros sulzeri*, Mammifère créodonte du Miocène d'Europe. *Ann. Paléontol. (Vert.)* 66(1):19–73.
- Ginsburg, L. 1982. Sur la position systématique du petit panda, *Ailurus fulgens* (Carnivora, Mammalia). *Géobios, Spéc. Mém.* 6:247–258.
- Ginsburg, L. 1983. Sur les modalités d'évolution du genre Néogène *Pseudaelurus* Gervais (Felidae, Carnivora, Mammalia). In: J. Chaline, ed. *Modalités, rythmes, mécanismes de l'évolution biologique: Gradualisme phylétique ou équilibres ponctuels?* CNRS Colloq. 330:131–136.
- Ginsburg, L., and Bulot, C. 1982. Les carnivores du Miocène de Bézian pres de la Romieu (Gers, France). *Proc. K. Nederland Akad. Wet.* (ser. B) 85(1):53–76.
- Ginsburg, L., and Morales, J. 1992. Contribution à la connaissance des Mustélidés (Carnivora, Mammalia) du Miocène d'Europe *Trochictis* et *Ischyriactis*, genres affines et genres nouveaux. *C. R. Acad. Sci. Paris* (ser. II) 315:111–116.
- Ginsburg, L., Le van Minh, Kieu Qui Nam, and Din van Thuan. 1992. Premières découvertes des vertébrés continentaux dans le Néogène du Nord du Vietnam. *C. R. Acad. Sci. Paris* (ser. II) 314:627–630.
- Gregory, W. K. 1936. On the phylogenetic relationships of the giant panda (*Ailuropoda*) to other arctoid Carnivora. *Amer. Mus. Novit.* 878:1–29.
- Guan, J. 1988. The Miocene strata and mammals from Tongxin, Ningxia and Guanghe, Gansu. *Mem. Beijing Nat. Hist. Mus.* 42:1–21.
- Gunnell, G., and Gingerich, P. 1991. Systematics and evolution of late Paleocene and early Eocene Oxyaenidae (Mammalia, Creodonta) in the Clark's Fork Basin, Wyoming. *Contrib. Mus. Paleontol., Univ. Michigan* 28(7):141–180.
- Gustafson, E. P. 1986. Carnivorous mammals of the Late Eocene and Early Oligocene of Trans-Pecos Texas. *Texas Memorial Mus. Bull.* 33:1–66.

- Harrison, T., Delson, E., and Guan, J. 1991. A new species of *Pliopithecus* from the middle Miocene of China and its implications for early catarrhine zoogeography. *J. Human Evol.* 21:329–361.
- Hendey, Q. B. 1974. The late Cenozoic Carnivora of the South-Western Cape Province. *Ann. South African Mus.* 63:1–369.
- Hendey, Q. B. 1978. Preliminary report on the Miocene vertebrates from Arrisdrift, South West Africa. *Ann. South African Mus.* 76(1):1–41.
- Hendey, Q. B. 1980. *Agriotherium* (Mammalia, Ursidae) from Langebaanweg, South Africa, and relationships of the genus. *Ann. South African Mus.* 81(1):1–109.
- Hershkovitz, P. 1972. The Recent mammals of the Neotropical region: A zoogeographic and ecological review. In: A. Keast, F. Erk, and B. Glass, eds. *Evolution, Mammals, and Southern Continents*, pp. 311–431. Albany: State Univ. New York Press.
- Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J. C., Behrensmeyer, A. K., Curtis, G., Jacobs, B. F., Jacobs, L., Johnson, N., and Pilbeam, D. 1985. Neogene paleontology and geochronology of the Baringo Basin, Kenya. *J. Human Evolution* 14:768.
- Hopwood, A., and Hollyfield, J. 1954. An annotated bibliography of the fossil mammals of Africa (1742–1950). *Fossil Mammals of Africa* No. 8, *British Mus. Nat. Hist.*, p. 136.
- Hough, J. R. 1944. The auditory region in some Miocene carnivores. *J. Paleontol.* 18(5):470–479.
- Hough, J. R. 1948. The auditory region in some members of the Procyonidae, Canidae, and Ursidae. *Bull. Amer. Mus. Nat. Hist.* 92(2):67–118.
- Hunt, R. M., Jr. 1974a. The auditory bulla in Carnivora: An anatomical basis for reappraisal of carnivore evolution. *J. Morphol.* 143(1):21–76.
- Hunt, R. M., Jr. 1974b. *Daphoenictis*, a cat-like carnivore (Mammalia, Amphicyonidae) from the Oligocene of North America. *J. Paleontol.* 48(5):1030–1047.
- Hunt, R. M., Jr. 1977. Basicranial anatomy of *Cynelos* Jourdan (Mammalia, Carnivora), an Aquitanian amphicyonid from the Allier Basin, France. *J. Paleontol.* 51(4):826–843.
- Hunt, R. M., Jr. 1987. Evolution of the aeluroid Carnivora: Significance of auditory structure in the nimravid cat *Dinictis*. *Amer. Mus. Novit.* 2886:1–74.
- Hunt, R. M., Jr. 1989. Evolution of the aeluroid Carnivora: Significance of the ventral promontorial process of the petrosal, and the origin of basicranial patterns in the living families. *Amer. Mus. Novit.* 2930:1–32.
- Hunt, R. M., Jr. 1990. Vascular countercurrent cooling mechanisms in Carnivora. *J. Vert. Paleontol.* 10(3, suppl.):28A.
- Hunt, R. M., Jr. 1991. Evolution of the aeluroid Carnivora: Viverrid affinities of the Miocene carnivoran *Herpestides*. *Amer. Mus. Novit.* 3023:1–34.
- Hunt, R. M., Jr. In press, a. North American Tertiary Ursidae. In: C. Janis, K. Scott, and L. Jacobs, eds. *The Tertiary Mammals of North America*. Cambridge: Cambridge Univ. Press.
- Hunt, R. M., Jr. In press, b. Basicranial anatomy of the giant viverrid from 'E' Quarry, Langebaanweg, South Africa. In: K. Stewart and K. Seymour, eds. *Paleoecology and Palaeoenvironments of Late Cenozoic Mammals: Tributes to the Career of C. S. Churcher*. Toronto: Univ. Toronto Press.
- Hunt, R. M., Jr. In press, c. North American Eocene-Oligocene Amphicyonidae. In: D. Prothero and R. J. Emry, eds. *The Terrestrial Eocene-Oligocene Transition in North America*. Cambridge: Cambridge Univ. Press.
- Hunt, R. M., Jr., and Barnes, L. 1994. Basicranial evidence for ursid affinity of the oldest pinnipeds. *Proc. San Diego Soc. Nat. Hist.* 29:57–67.

- Hunt, R. M., Jr., and Skolnick, R. I. In press. The giant mustelid *Megalictis* from the early Miocene carnivore dens at Agate Fossil Beds National Monument, Nebraska: Earliest evidence of dimorphism in New World Mustelidae (Carnivora, Mammalia). *Univ. Wyoming Contrib. Geol.*
- Hunt, R. M., Jr., and Solounias, N. 1991. Evolution of the aeluroid Carnivora: Hy-aenid affinities of the Miocene carnivoran *Tungurictis spocki* from Inner Mongolia. *Amer. Mus. Novit.* 3030:1–25.
- Hunt, R. M., Jr., and Tedford, R. H. 1993. Phylogenetic relationships within the aeluroid Carnivora and implications of their temporal and geographic distribution. In: F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds. *Mammal Phylogeny (Placentals)*, pp. 53–73. New York: Springer-Verlag.
- Kruuk, H. 1972. *The Spotted Hyena*. Chicago: Univ. Chicago Press.
- Kurtén, B. 1966. Pleistocene bears of North America, 1: Genus *Tremarctos*, spectacled bears. *Acta Zool. Fennica* 115:1–120.
- Kurtén, B. 1967. Pleistocene bears of North America, 2: *Arctodus*, short-faced bears. *Acta Zool. Fennica* 117:1–60.
- Kurtén, B., and Anderson, E. 1980. *Pleistocene mammals of North America*. New York: Columbia Univ. Press.
- Lange-Badré, B. 1979. Les créodontes (Mammalia) d'Europe occidentale de l'Éocène supérieur à l'Oligocène supérieur. *Mem. Mus. nat. Hist. natl., Paris* (ser. C) 42:1–249.
- Lange-Badré, B., and Haubold, H. 1990. Les créodontes (mammifères) du gisement du Geiseltal (Éocène Moyen, RDA). *Géobios* 23(5):607–637.
- Lavocat, R. 1951. Sur les affinités de quelques carnassiers de l'Oligocène d'Europe, notamment du genre *Plesictis* et du genre *Proailurus*. *C. R. Soc. Paléont. Suisse, Ecol. Géol. Helv.* 44(2).
- Lavocat, R. 1952. Sur les affinités de quelques carnassiers de l'Oligocène d'Europe, notamment du genre *Plesictis* Pomel et du genre *Proailurus* Filhol. *Mammalia* 16:62–72.
- Li C., Lin Y., Gu Y., Hou L., Wu W., and Qiu Z. 1983. The Aragonian vertebrate fauna of Xiacaowan, Jiangsu. *Vert. Palasiatica* 21(4):313–327.
- Li C., Wu W., and Qiu Z. 1984. Chinese Neogene: Subdivision and Correlation. *Vert. Palasiatica* 22(3):163–178.
- Marshall, L. G. 1976. Evolution of the family Thylacosmilidae, fossil marsupial sabertooths of South America. *Paleobios* 23:1–20.
- Marshall, L. G. 1978a. Evolution of the Borhyaenidae, extinct South American predaceous marsupials. *Univ. California Publ. Geol. Sci.* 117:1–89.
- Marshall, L. G. 1978b. The Terror Bird. *Field Mus. Nat. Hist. Bull.* 49(9):6–15.
- Marshall, L. G. 1981. The families and genera of Marsupialia. *Fieldiana: Geol.* (n.s.) 8:1–65.
- Marshall, L. G. 1985. Geochronology and land mammal biochronology of the trans-american faunal interchange. In: F. Stehli and S. D. Webb, eds. *The Great American Biotic Interchange*, pp. 49–85. New York: Plenum Press.
- Marshall, L., Berta, A., Hoffstetter, R., Pascual, R., Reig, O., Bombin, M., and Mones, A. 1984. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Quaternary of South America. *Palaeovertebrata: Mém. Extraord.* 1984:1–76.
- Marshall, L., Hoffstetter, R., and Pascual, R. 1983. Mammals and stratigraphy: Geochronology of the continental mammal-bearing Tertiary of South America. *Palaeovertebrata: Mém. Extraord.* 1983:1–93.
- Marshall, L., and Sempere, T. 1993. Evolution of the Neotropic Cenozoic land mammal fauna in its geochronologic, stratigraphic, and tectonic context. In: P. Goldblatt,

- ed. *Biological Relationships between Africa and South America*, pp. 329–392. New Haven, Conn.: Yale Univ. Press.
- Matthew, W. D. 1909. The Carnivora and Insectivora of the Bridger Basin, middle Eocene. *Amer. Mus. Nat. Hist. Memoir* 9:289–567.
- Matthew, W. D. 1924. Third contribution to the Snake Creek fauna. *Bull. Amer. Mus. Nat. Hist.* 50(2):59–210.
- Meade, G. E. 1961. The sabertoothed cat *Dinobastis serus*. *Bull. Texas Mem. Mus.* 2(2):23–60.
- Mein, P. 1958. Les mammifères de la faune sidérolithique de Vieux-Collonges. *Nouv. Arch. Mus. Hist. Nat., Lyon* 5:1–122.
- Mein, P. 1989. Updating of MN zones. In: E. H. Lindsay, V. Fahlbusch, and P. Mein, eds. *European Neogene Mammal Chronology*, pp. 73–90. New York: Plenum Press.
- Mellet, J. S. 1977. Paleobiology of North American *Hyaenodon* (Mammalia, Creodonta). *Contrib. Vert. Evol.* 1:1–134.
- Merriam, C. 1930. *Allocyon*, a new canid genus from the John Day beds of Oregon. *Univ. California Publ. Geol. Sci.* 19:229–244.
- Mitchell, E. 1975. Parallelism and convergence in the evolution of the Otariidae and Phocidae. *Rapp. P.-v. Réun. Cons. Intl. Explor. Mer.* 169:12–26.
- Mitchell, E., and Tedford, R. H. 1973. The Enaliarctinae: A new group of extinct aquatic Carnivora and a consideration of the origin of the Otariidae. *Bull. Amer. Mus. Nat. Hist.* 151(3):201–284.
- Neff, N. 1983. The basicranial anatomy of the Nimravidae (Mammalia: Carnivora): Character analyses and phylogenetic inferences. Ph.D. dissert., City University of New York.
- Neff, N., and Coheleach, G. 1982. *The Big Cats (The Paintings of Guy Coheleach)*. New York: Harry Abrams.
- Nowak, R. M. 1991. *Walker's Mammals of the World*, 5th Ed. Baltimore: Johns Hopkins Univ. Press, Vol. 2 (pp. 643–1629).
- Olson, E. C., and McGrew, P. O. 1941. Mammalian fauna from the Pliocene of Honduras. *Bull. Geol. Soc. Amer.* 52:1219–1244.
- Opdyke, N. D., Lindsay, E. H., Johnson, N. M., and Downs, T. 1977. The paleomagnetism and magnetic polarity stratigraphy of the mammal-bearing section of Anza-Borrego State Park, California. *Quaternary Res.* 7:316–329.
- Patterson, B., and Pascual, R. 1972. The fossil mammal fauna of South America. In: A. Keast, F. Erk, and B. Glass, eds. *Evolution, Mammals, and Southern Continents*, pp. 247–309. Albany: State Univ. New York Press.
- Paule, W. J., and Baker, M. A. 1978. Structural basis for heat-exchanger function of the carotid rete in the cat. *Anat. Rec.* 190:505.
- Petter, G. 1967. *Paragale hürzeleri* nov. gen., nov. sp., mustélide nouveau de l'Aquitainien de l'Allier. *Bull. Soc. géol. France* (7e ser.) 9:19–23.
- Petter, G. 1969. Interprétation évolutive des caractères de la dentures des viverridés africains. *Mammalia* 33:607–625.
- Petter, G. 1976. Étude d'un nouvel ensemble de petits carnivores du Miocène d'Espagne. *Géol. Mediterr.* 3(2):135–154.
- Petter, G. 1987. Small carnivores (Viverridae, Mustelidae, Canidae) from Laetoli. In: M. D. Leakey and J. M. Harris, eds. *Laetoli: A Pliocene Site in Northern Tanzania*, pp. 194–234. Oxford: Clarendon Press.
- Pocock, R. I. 1916. The tympanic bulla in hyaenas. *Proc. Zool. Soc. London* 1916:303–307.
- Pocock, R. I. 1921. The external characters and classification of the Procyonidae. *Proc. Zool. Soc. London* 1921:389–422.
- Pocock, R. I. 1929. The structure of the auditory bulla in the Procyonidae and the

- Ursidae, with a note on the bulla of *Hyaena*. *Proc. Zool. Soc. London* 1929:963–974.
- Qiu Z.-X. 1989. The Chinese Neogene mammalian biochronology: Its correlation with the European Neogene mammalian zonation. In: E. H. Lindsay, V. Fahlbusch, and P. Mein, eds. *European Neogene Mammal Chronology*, pp. 527–556. New York: Plenum Press.
- Qiu Z.-X., and Qi G. 1989. Ailuropod found from the late Miocene deposits in Lufeng, Yunnan. *Vert. Palasiatica* 27:153–169.
- Qiu Z.-X. and Qiu Z.-D. 1990. Late Tertiary mammalian local faunas of China. *J. Stratigraphy* 14(4):241–260.
- Qiu Z.-X., Xie J., and Yan D. 1988a. Discovery of the skull of *Dinocrocuta gigantea*. *Vert. Palasiatica* 26:128–138.
- Qiu Z.-X., Ye J., and Cao J. 1988b. A new species of *Percrocuta* from Tongxin, Ningxia. *Vert. Palasiatica* 26:116–127.
- Rawn, V. M. 1981. Scimitar cats, *Homotherium serum* Cope, from Gassaway fissure, Cannon County, Tennessee, and the North American distribution of *Homotherium*. *J. Tennessee Acad. Sci.* 56(1):15–19.
- Reig, O. 1952. Sobre la presencia de mustelidos mefitinos en la formacion de Chapadmalal. *Rev. Mus. Mun. Cien. Nat. Trad. Mar del Plata* 1:45–51.
- Remy, J. A., et al. (nine others). 1987. Biochronologie des Phosphorites du Quercy: Mise à jour des listes fauniques et nouveaux gisements de mammifères fossiles. *München Geowiss. Abhandl.* 10:169–188.
- Repenning, C. A. 1976. Adaptive evolution of sea lions and walruses. *Syst. Zool.* 25(4):375–390.
- Repenning, C. A., Ray, C. E., and Grigorescu, D. 1979. Pinniped biogeography. In: J. Gray and A. Boucot, eds. *Historical Biogeography, Plate Tectonics, and the Changing Environment*, pp. 357–369. Corvallis: Oregon State Univ. Press.
- Repenning, C. A., and Tedford, R. H. 1977. Otarioid Seals of the Neogene. *U.S. Geol. Surv. Prof. Paper* 992:1–93.
- Riggs, E. S. 1934. A new marsupial sabertooth from the Pliocene of Argentina and its relationships to other South American predaceous marsupials. *Trans. Amer. Phil. Soc. (n.s.)* 24:1–31.
- Roberts, M., and Gittleman, J. 1984. *Ailurus fulgens*. *Mammal. Species* 222:1–8.
- Russell, D., and Zhai R.-J. 1987. The Paleogene of Asia: Mammals and stratigraphy. *Mem. Mus. Natl. d'Hist. Natur., Sci. de la Terre (ser. C)* 52:1–488.
- Savage, R. J. G. 1965. Fossil mammals of Africa. 19: The Miocene Carnivora of East Africa. *Bull. British Mus. (Nat. Hist.), Geol.*, 10(8):239–316.
- Savage, R. J. G. 1989. The African dimension in European early Miocene mammal faunas. In: E. H. Lindsay et al., eds. *European Neogene Mammal Chronology*, pp. 587–599. New York: Plenum Press.
- Schmidt-Kittler, N. 1981. Zur Stammesgeschichte der marderverwandten Raubtiergruppen (Musteloidea, Carnivora). *Ecol. Geol. Helvet.* 74(3):753–801.
- Schmidt-Kittler, N. 1983. On a new species of *Sivanasua* Pilgrim 1931 (Feliformia, Carnivora) and the phylogenetic position of this genus. *Proc. Konin. Nederl. Akad. Wetensch. (ser. B)* 86(3):301–318.
- Schmidt-Kittler, N. 1987. The Carnivora (Fissipedia) from the Lower Miocene of East Africa. *Palaeontographica (Abt. A)* 197:85–126.
- Scott, W. B. 1938. A problematical cat-like mandible from the Uinta Eocene, *Apataelurus kayi* Scott. *Annals Carnegie Mus.* 27:113–120.
- Segall, W. 1943. The auditory region of the arctoid carnivores. *Fieldiana: Zool.* 29(3):33–59.

- Simpson, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.* 85:1–350.
- Springhorn, R. 1980. Radiation der Hyaenodonta (Mammalia, Deltatheridia) unter gebiss-strukturellen Gesichtspunkten und ein Vergleich mit fissipeden Carnivora. *Ber. Naturf. Ges. Freiburg i. Br.* 70:97–109.
- Stehlin, H. G. 1925. Catalogue des ossements de mammifères tertiaires de la collection Bourgeois à l'École de Pont-Levoy (Loir-et-Cher). *Bull. Soc. Hist. Nat. Anthropol. Loir-et-Cher* 18:77–277.
- Stirton, R. A. 1960. A marine carnivore from the Clallam Miocene Formation, Washington. *Univ. California Publ. Geol. Sci.* 36(7):345–368.
- Tchernov, E., Ginsburg, L., Tassy, P., and Goldsmith, N. 1987. Miocene mammals from the Negev (Israel). *J. Vert. Paleontol.* 7(3):284–310.
- Tedford, R. H. 1976. Relationships of pinnipeds to other carnivores (Mammalia). *Syst. Zool.* 25(4):363–374.
- Tedford, R. H., Barnes, L. G., and Ray, C. E. 1991. Earliest Miocene littoral arctoid *Kolponomos*. *J. Vert. Paleontol.* 11(3):57A.
- Tedford, R. H., and Gustafson, E. 1977. First North American record of the extinct panda *Parailurus*. *Nature* 265(5595):621–623.
- Teilhard de Chardin, P. 1915. Les carnassiers des Phosphorites du Quercy. *Ann. Paléontol.* 9(3–4):103–192.
- Thomas, H., Sen, S., Khan, M., Battail, B., and Ligabue, G. 1982. The lower Miocene fauna of Al-Sarrar (Eastern Province, Saudi Arabia). *ATLAL, J. Saudi Arabian Archaeol. Jeddah* 5:109–136.
- Turnbull, W. D., and Segall, W. 1984. The ear region of the marsupial sabertooth, *Thylacosmilus*: Influence of the sabertooth lifestyle upon it, and convergence with placental sabertooths. *J. Morphol.* 181:239–270.
- Turner, H. N. 1848. Observations relating to some of the foramina at the base of the skull in Mammalia, and on the classification of the Order Carnivora. *Proc. Zool. Soc. London* 1848:63–88.
- Van Valen, L. 1969. The multiple origins of the placental carnivores. *Evolution* 23(1):118–130.
- Viret, J. 1929. Les faunes des mammifères de l'Oligocène supérieur de la Limagne Bourbonnaise. *Ann. l'Univ. Lyon* (n.s.) 47:1–328.
- Webb, S. D., and Perrigo, S. C. 1984. Late Cenozoic vertebrates from Honduras and El Salvador. *J. Vert. Paleontol.* 4(2):237–254.
- Werdelin, L., and Solounias, N. 1991. The Hyaenidae: Taxonomy, systematics and evolution. *Fossils and Strata* 30:1–104.
- Whitmore, F. C., Jr., and Stewart, R. H. 1965. Miocene mammals and Central American seaways. *Science* 148:180–185.
- Whybrow, P. J. 1987. Miocene geology and paleontology of Ad Dabtiyah, Saudi Arabia: Summary. *Bull. British Mus. (Nat. Hist.)* 41(4):367–369.
- Wurster, D., and Benirschke, K. 1968. Comparative cytogenetic studies in the Order Carnivora. *Chromosoma* 24:336–382.
- Wyss, A. R. 1987. The walrus auditory region and the monophyly of pinnipeds. *Amer. Mus. Novit.* 2871:1–31.
- Wyss, A. R., and Flynn, J. J. 1993. A phylogenetic analysis and definition of the Carnivora. In: F. S. Szalay, M. J. Novacek, and M. C. McKenna, eds. *Mammal Phylogeny (Placentals)*, pp. 32–52. New York: Springer-Verlag.